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A Synopsis of the Flat Bugs (Heteroptera: Aradidae) of Michigan

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Abstract

An overview of the 28 species of Aradidae found in Michigan is presented, along with an identification key, distribution maps, and relevant literature. Eleven new state records are presented for the following species: *Aradus approximatus* Parshley, *Aradus duzeei* Bergroth, *Aradus falleni* Stål, *Aradus insolitus* Van Duzee, *Aradus intectus* Parshley, *Aradus montanus* Bergroth, *Aradus proboscideus* Walker, *Aradus shermani* Heidemann, *Aradus uniformis* Heidemann, *Quilnus niger* (Stål) (all Aradinae), and *Neuroctenus simplex* (Uhler) (Mezirinae).

Keywords. true bugs, faunistics, distribution, checklist

Aradidae, commonly called flat bugs or bark bugs, is a family of strongly flattened mycophagous true bugs comprising 126 species in 11 genera in the United States (updated from Froeschner 1988). These insects are cryptic both in habitus and habitat, having a granular integument that adheres bits of substrate and being found most often under the bark of dead or dying trees or logs. They also tend to be slow-moving insects, and this habit, coupled with habitus and habitat, can make them difficult to see, even when (unknowingly) encountered. Thus, despite being a diverse group, aradids are uncommonly found, especially compared to other Heteroptera, and this phenomenon is apparent in the holdings of entomological research collections.

The group has never been treated for Michigan, although O'Brien's (1983, 1988) lists of literature concerning the terrestrial arthropods of Michigan contain sources with a few records of Aradidae. Townsend (1890) and Hussey (1922) contributed to the knowledge of the Aradidae of Michigan, each having catalogued the Heteroptera found in the vicinity of Constantine, Saint Joseph County and Berrien County, respectively. Additionally, Pettit (1901) recorded an *Aradus* sp. from Munising Junction (Alger County), and Adams (1909) recorded a single species of *Aradus* from Isle Royale (Keweenaw County). One species, *Aradus ruficeps* Hussey, 1953, was described based on a single specimen from Michigan.

In an effort to compile the knowledge and expose the diversity of these cryptic insects, I herein present the results of my study of the Aradidae of Michigan, my seventh synoptic family-level contribution studying the heteropteran fauna of the state.

Materials and Methods. Methods parallel previous installments of this series (Swanson 2011, 2012a, b, 2013, 2015, 2016):

The aradid holdings of the two major university collections in southern Michigan were examined. County records were compiled, identification keys were modified, and the existing natural history information, both Michiganian and extralimital, was summarized. Notes on additional species of potential relevance to Michigan follow the primary species accounts.

The identification of the 282 specimens included in this study was rendered or confirmed by the author, and all specimens reside in one of the collections listed below unless otherwise noted. Collection dates indicate the earliest and latest adults examined and refer specifically to specimens collected in Michigan. In the instances where provided, label data are not transcribed verbatim, but complete locality information is included. Any additions, changes, or interpretive

Figure 1. The counties of the State of Michigan.

elements provided by the author are shown in brackets. Locations of Michigan counties from which specimens were collected are depicted in Fig. 1.

The habitus plates (Figs. 2–4) are intended to provide a visual reference for the diversity found in Michigan. Several forms are distinctive in general habitus or particular morphological characters. However, comparison with the plates will not serve as a replacement for keying out specimens.

In the keys, certain characters are occasionally set apart using brackets. These brackets signify that the contrasting character is not in that particular couplet but appears in one of the immediately successive couplets attained through the opposite lead.

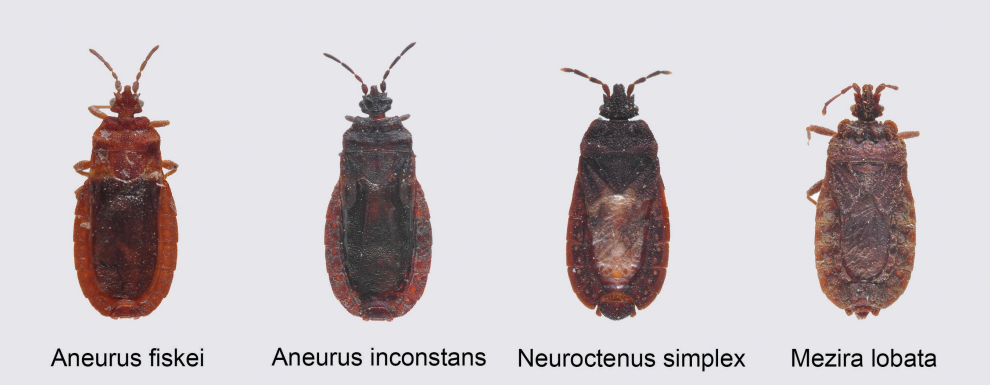


Figure 2. Aneurinae and Mezirinae of Michigan, dorsal habitus.

Regarding host records, I have compiled those previously mentioned in the literature for the aradid species found in Michigan (Table 2), with a few caveats. First, I have reduced records of trees to genus-level only; this means that tree species *might* be listed in the original citation. Second, I have included only tree genera that occur in Michigan. For example, in addition to the five genera listed in the table, *Aneurus fiskei* Heidemann, 1904a also has been recorded from *Oxydendrum* [*arboreum* (L.) DC.] (Blatchley 1926); yet, this record is herein excluded, because sourwood does not occur in Michigan. In the case where an aradid has been recorded from a tree species absent in Michigan but with congeners that are present in the state, I have included the generic level record. For example, *Quilnus niger* (Stål, 1873) has been recorded from longleaf pine (*Pinus palustris* Mill.) (Parshley 1921), and even though longleaf pine does not occur in Michigan, *Pinus* is still marked in the table, regardless of whether records for other *Pinus* spp. exist for *Q. niger* (they do!). Presence of tree genera and species in Michigan was assessed using Barnes and Wagner (2004). The compilation of this table should not be construed as a definitive statement on the hosts of aradids. On the contrary, there is little evidence to suggest that aradids are restricted to particular species of trees, and many of these records represent at best (1) trees that can host fungal species consumed by aradids or (2) incidental captures, especially if occurring during seasonal flights. Lastly, records of fungal hosts, being much more sparse (and perhaps more meaningful) are listed under the species accounts.

Collections are designated as follows: Daniel R. Swanson, personal collection (DRS); Albert J. Cook Arthropod Research Collection, Michigan State University, East Lansing, Michigan (MSUC); and University of Michigan Museum of Zoology Insect Collection, Ann Arbor, Michigan (UMMZ).

Results and Discussion

Family ARADIDAE Spinola, 1837

Flat bugs are generally unmistakable in their oval to rectangular, strongly-flattened habitus. Additionally, members in the Nearctic may be characterized by a short, stout four-segmented rostrum, absence of ocelli, two-segmented tarsi, and a rough or granular integument (Slater and Baranowski 1978, Schuh and Slater 1995). Aradids also possess distinctive coiled mandibular stylets, thereby allowing long structures to be stored in a small head capsule (Spooner 1920, Lee and Pendergrast 1976). Aradids are usually found under the bark or on fungus associated with dead or dying trees or in leaf litter. However, some members of the family are found in the nests of birds and rodents, as well as termites (Kormilev and Froeschner 1987, Schuh and Slater 1995). Some species are gregarious (Cassis and Gross 2002), with many individuals of various life stages found in groups under a single patch of bark. Others go beyond simple gregariousness: McClure (1932), Takahashi (1934), and Taylor (1988a) described parental care in three different aradid species. However, it is not known how widely this phenomenon occurs in the family. Stridulation also is documented in the group (Bergroth 1892, Usinger 1954). Leston (1955) generally described the male and female genitalia. Vásárhelyi (1986) investigated the utility of the pretarsus as a taxonomic character. Schuh and Slater (1995) provided a concise general family-level treatment in a systematic context.

Aradids are predominantly fungus-feeders. Hubbard (1892) provided one

Figure 3. Aradinae of Michigan, dorsal habitus.

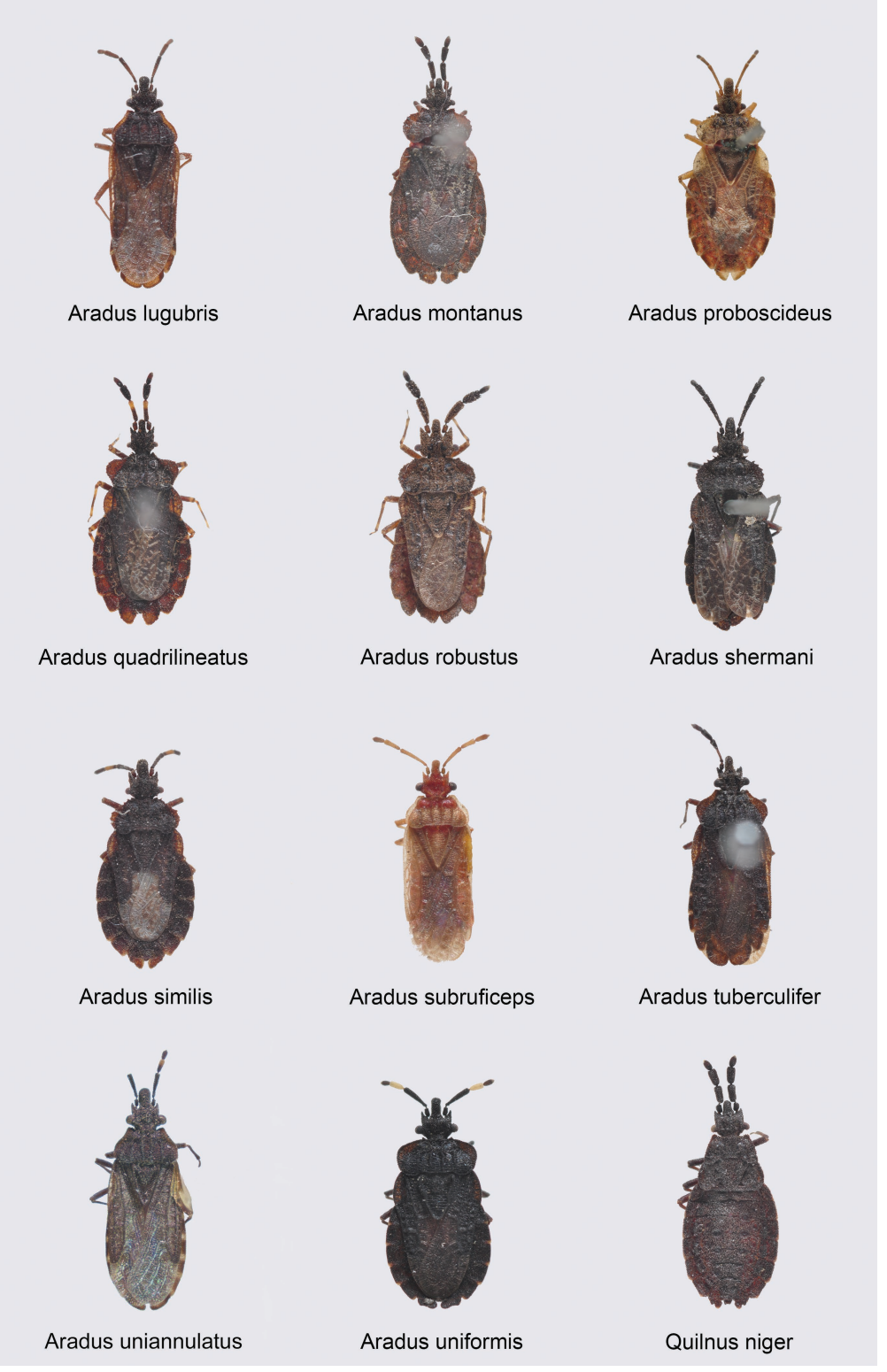


Figure 4. Aradinae of Michigan (cont.), dorsal habitus.

Table 1. Species of Aradidae found in Michigan.

Aneurinae
Aneurus fiskei **Heidemann, 1904a**
Aneurus inconstans **Uhler, 1871**
Aradinae
Aradus abbas **Bergroth, 1889**
Aradus acutus **Say, 1831**
Aradus aequalis **Say, 1831**
Aradus approximatus **Parshley, 1921**
Aradus borealis **Heidemann, 1909**
Aradus crenatus **Say, 1831**
Aradus duzeei **Bergroth, 1892**
Aradus falleni **Stål, 1860**
Aradus implanus **Parshley, 1921**
Aradus inornatus **Uhler, 1876**
Aradus insolitus **Van Duzee, 1916**
Aradus intectus **Parshley, 1921**
Aradus lugubris **Fallén, 1807**
Aradus montanus **Bergroth, 1913**
Aradus proboscideus **Walker, 1873**
Aradus quadrilineatus **Say, 1825**
Aradus robustus **Uhler, 1871**
Aradus shermani **Heidemann, 1906**
Aradus similis **Say, 1831**
Aradus subruficeps **Hussey, 1953**
Aradus tuberculifer **Kirby, 1837**
Aradus uniannulatus **Parshley, 1921**
Aradus uniformis **Heidemann, 1904b**
Quilnus niger **(Stål), 1873**
Mezirinae
Mezira lobata **(Say, 1831)**
Neuroctenus simplex **(Uhler, 1876)**

of the earlier accounts of this behavior, suggesting that the rough surface of these insects provided surfaces for the transport of fungal spores. Schwartz (1901) later split the group between a preference for "feed[ing] upon a blackish mould under the bark" and "liv[ing] outside of the bark of dead trees, upon a whitish fungus". Many subsequent authors (e.g., Parshley 1921, Blatchley 1926, Jordan 1932, Usinger 1936) have corroborated mycophagous behavior. Furthermore, one species, *Aradus kormilevi* Heiss, 1980, has been found in association with the southern pine beetle *Dendroctonus frontalis* Zimmermann, 1868 (Overgaard 1968, Moser et al. 1971; both reported the species as *Aradus cinnamomeus* Panzer, 1806), a bark beetle that often introduces fungal pathogens into the tree (Bramble and Holst 1940, Paine et al. 1997). It also was hypothesized that even those nidicolous species still feed on fungi present in the nests and burrows (Usinger 1936). Nevertheless, a few species may develop on non-tree plants (Tamanini 1955, Heiss 1984), a few subfamilies may subsist on tree sap (Schuh and Slater 1995), and a single Palearctic species is known to feed on phloem, cambium, and xylem of healthy trees (Kormilev and Froeschner 1987). This latter species, *A. cinnamomeus*, is the only aradid known to be pestiferous (Heliövaara 2000).

Despite their slow-moving ways and cryptic habitat, aradids are surprisingly strong dispersers. There is a high incidence of wing polymorphism in the family (Usinger and Matsuda 1959, Kormilev and Froeschner 1987). In general, polymorphism seems driven by competing needs to maneuver in tight subcorticolous habitats and to disperse to new sites given the ephemeral nature of their food and habitat; indeed, seasonal dispersal flights are well-documented in the group, e.g., McPherson and Weber (1981). Other stimuli seem to draw aradids. Various species are known to be pyrophilous, viz. attracted to forest fires or recently burned trees (e.g., Wyniger et al. 2002, Hjältén et al. 2006, Johansson et al. 2010), and these species often possess specialized sensilla to aid in locating these phenomena (Schmitz et al. 2010). Studies have shown that some aradids engage in scototaxis (Heliövaara and Terho 1981, Taylor 1988b), although some species also are, at least indirectly, attracted to lights at night (Usinger and Matsuda 1959). Still, complete aptery is well-known, independently-derived in several lineages, and concentrated in the Tropics, likely a result of high abundance of food and habitat in these moist ecosystems (Monteith 1982). However, no apterous species have ever been associated with non-apterous morphs (Kormilev and Froeschner 1987). Yet, every other condition, i.e., macroptery, brachyptery, stenoptery, and microptery, is exhibited by some species of aradid, and some species display several of these conditions in a single population (e.g., Heliövaara 1984). Additionally, some macropterous aradids are known to purposefully induce brachyptery "by spontaneous shedding or by self-mutilation" (Kormilev and Froeschner 1987; see also Kenward 1975), a condition termed "ruptobrachyptery" by Kormilev and Froeschner (1987). In another regard to dispersal, aradids may be somewhat pagile, given that several species present in the New World (i.e., *Aradus lugubris* Fallén, 1807; *Aradus signaticornis* Sahlberg, 1848) were described from the Palearctic (Froeschner 1988). However, in contrast to other live-wood-boring insects (e.g., Buprestidae, Cerambycidae, Curculionidae), pagility among Aradidae may be mitigated in that

Table 2. Host records for species of Aradidae found in Michigan. Records marked with an asterisk (*) are not novel but were reported in earlier references that I have not located.

	Abies	*Juniperus*	*Picea*	*Pinus*	*Taxodium*	*Tsuga*	*Acer*	*Betula*	*Carpinus*	*Carya*	*Crataegus*	*Fagus*	*Fraxinus*	*Liriodendron*	*Platanus*	*Populus*	*Quercus*	*Salix*	*Talia*	*Ulmus*	*Xanthoxylum*
Aneurus fiskei									5			9			4		5				10
An. inconstans	14						13*	1				11									
Aradus abbas				8*	8*																
Ar. acutus																	4,8, 10, 15	15			
Ar. approximatus				8, 10, 16																	
Ar. crenatus	8*						4, 10	8*	13*	4	13*	8*		4, 10	8, 10	16	8*, 10	13*			
Ar. duzeei				8			10					10									
Ar. falleni				7																	
Ar. implanus																				9	
Ar. insolitus																13*, 16		13*			
Ar. lugubris		8*	8*	8*			1, 10												13*		
Ar. proboscideus	12		8	8, 12																	
Ar. quadrilineatus												10, 11				14	8, 10 16			14	
Ar. robustus						11						9,11					8, 10				
Ar. similis				10			4, 10	8, 10					10				10			4, 10	
Ar. uniannulatus				13*																	
Ar. uniformis				8																	
Quilnus niger				2,4, 8, 15		**14**															
Mezira lobata																	10			10	
Neuroctenus simplex				6, 10								3					3-5, 10 15, 16				

[1]Van Duzee (1894)
[2]Heidemann (1901)
[3]Osborn (1903)
[4]Heidemann (1904a)
[5]Torre-Bueno (1908)
[6]Heidemann (1909)
[7]Van Duzee (1916)
[8]Parshley (1921)
[9]Hussey (1922)
[10]Blatchley (1926)
[11]Torre-Bueno (1935)
[12]Usinger (1936)
[13]Usinger and Matsuda (1959, Table 1)
[14]Matsuda (1977)
[15]Taylor and McPherson (1989)
[16]Present study

flat bugs typically require dead or decaying wood, which is generally a product of low commercial or shipping value.

Little is known about the predators of flat bugs. Presumably other subcorticolous arthropods, particularly ants and beetles, prey on aradids, although this has never been recorded in the literature (Usinger and Matsuda 1959). However, Blatchley (1926) noted a female *Aradus similis* Say, 1831 heavily infested under the hemelytra with the mite *Cheyletus clavispinus* Banks, 1902. Furthermore, there are several hymenopterans known to parasitize flat bugs or their eggs, notably platygastrids in the genus *Aradophagus* Ashmead, 1893 (Heidemann 1904a) and *Telenomus aradi* Kozlov, 1967 (Heliövaara et al. 1982).

Flat bugs are strongly affected, often negatively so, by human interactions with trees and/or forests (Osborn 1903, Parshley 1924, Johansson et al. 2010), a conclusion easy to reach given aradids' stenophagy and the increased anthropogenic destruction of virgin habitat over the last several centuries. In one study, Heliövaara and Väisänen (1983) documented that human disturbance caused proliferation in only one aradid species, whereas five others severely declined. From the other side, another study showed that approximating natural disturbances, such as through prescribed burning, increased the diversity and abundance of aradid species in forest stands (Hägglund et al. 2015). Heliövaara et al. (1983) documented positive and negative effects on population growth of one Finnish species correlated with nitrogen fertilization and insecticide use, respectively, in forest plots. Furthermore, it will be important to better elucidate the ranges and host preferences of individual species in order to focus conservation efforts and better preserve aradid diversity.

At the family-level, the taxonomy of the group has remained somewhat stable, at least in the Nearctic. Aradidae, together with Termitaphididae, form the superfamily Aradoidea, although the latter family is not known to occur in the United States or Canada. However, several of the subfamilies had previously been treated as distinct families, i.e., Aneuridae, Meziridae. The most current catalog for the taxa found in America north of Mexico was provided by Froeschner (1988), although Kormilev and Froeschner's (1987) world catalog also contains those species. In Aradidae, three of five subfamilies found in the Nearctic region are represented in Michigan; Calisiinae and Carventinae are known in the U.S. only from the Gulf States. Of taxa in the three present subfamilies, 28 species in 5 genera are found in the state (Table 1).

For the species found north of Mexico, Parshley's (1921, 1929) monograph, a chapter in Blatchley's (1926) tome on eastern Heteroptera, and Torre-Bueno's (1939) synopsis are early but still useful references for the group. Additionally, despite their broader scope, both Usinger and Matsuda's (1959) systematic treatment and Kormilev and Froeschner's (1987) global catalog still provide much useful biological and biogeographical information relevant to the Nearctic taxa. Undoubtedly, Matsuda's (1977) synopsis of the Canadian species remains the most useful work for identification of boreal species in the New World. The following key was synthesized from Parshley (1921), Blatchley (1926), Torre-Bueno (1939), and Matsuda (1977).

Key to the Aradidae of Michigan

1 Postocular area distinctly wider than anteocular area; eyes scarcely or very slightly prominent beyond postocular area; scape with base barely, or less abruptly, narrowed; trochanters freely-articulating with femora; abdominal spiracles remote from basal margins of ventrites 2

1' Postocular area scarcely wider than anteocular area; eyes very prominent beyond postocular area; scape short, stout, base suddenly narrowed into an extremely short, oblique style; trochanters connate with femora; abdominal spiracles placed near basal margins of ventrites (Aradinae) 5

2 (1) Scutellum transverse, obtusely rounded, broad apically; fourth antennomere much longer than third; rostral groove lanceolate (Aneurinae: *Aneurus*).....3

2' Scutellum triangular, hardly transverse; fourth antennomere not, or but slightly, longer than third, generally shorter; rostral groove linear (Mezirinae).....4

3 (2) Pedicel obovate or subobovate, more similar in shape to scape than third antennomere; fourth antennomere twice as long as third; size smaller, 3.5–4 mm .....*Aneurus fiskei*

3' Pedicel elongate, cylindrical, more similar to third antennomere than scape; fourth antennomere one third or less longer than third; size larger, 5.5–6.5 mm .....*Aneurus inconstans*

4 (2') Anterior margin of fourth, fifth, and sixth abdominal ventrites lacking ventral ridge; third antennomere conspicuously longer than second (*Mezira*) .....*Mezira lobata*

4' Fourth, fifth, and sixth abdominal ventrites with narrow, sharp, transverse ventral ridge behind anterior margin; third antennomere, at most, only slightly longer than second (*Neuroctenus*) ..... *Neuroctenus simplex*

5 (1') Rostrum not extending beyond base of head; pronotum trapezoidal, not explanate laterally (*Quilnus*) .....*Quilnus niger*

5' Rostrum extending beyond base of head; pronotal shape variable but margins more or less explanate laterally (*Aradus*) 6

6 (5') Pedicel as long as or slightly longer than third antennomere 7

6' Pedicel distinctly longer than third.....8

7 (6) Pronotum widest behind middle; pronotal margin smooth, untoothed; connexival margin more-or-less entire..... *Aradus aequalis*

7' Pronotum widest before middle; pronotal margin denticulate in anterior half; connexival margin crenate..... *Aradus crenatus*

8 (6') Third antennomere one-half thicker than pedicel; pedicel conspicuously bicolorous, blackish in basal half, pale yellowish in apical half .....*Aradus quadrilineatus*

8' Third antennomere as thick as or only slightly thicker than pedicel; pedicel rarely bicolorous, if so and paler apically, then yellow only at extreme apex.....9

9 (8') Lateral margin of pronotum distinctly sinuate in anterior half, distinctly angularly-produced behind middle; rostrum reaching middle of prosternum .....*Aradus insolitus*

9' Lateral margin of pronotum may be sinuate in anterior half, but not angularly produced behind middle; rostrum usually extending beyond middle of prosternum.....10

10 (9') Antennae robust, widest point distinctly thicker than profemur; [pedicel distinctly less than twice as long as third; third antennomere not pale, generally concolorous with other antennomeres].....11

10' Antennae more slender, greatest width subequal to or thinner than profemoral thickness 14

11 (10) Scutellum pentagonal, bases parallel-sided; fourth antennomere small, about half-width of incrassate third..... *Aradus robustus*

11' Scutellum more-or-less triangular, bases convergent; fourth antennomere subequal to or slightly thinner than third 12

12 (11') Pedicel distinctly shorter than interocular distance; only brachypterous form known..... *Aradus intectus*

12' Pedicel subequal to or slightly longer than interocular distance; only macropterous form known 13

13 (12') Pronotum unicolorous; scape yellow-brown, contrasting dark-brownish second and third antennomeres..... *Aradus duzeei*

13' Pronotum with pale spot along anterolateral margin; scape dark-brown, more similar in color to subsequent two antennomeres .....*Aradus implanus*

14 (10') Corium with lateral margins straight, more-or-less parallel-sided, not distinctly dilated at base; [pronotal margins entire, at most, evenly granulate] (*lugubris* group) 15

14' Corium dilated laterally at base 19

15 (14) Pedicel long, slender, cylindrical, greater than twice length of third antennomere; corium wholly opaque; [third antennomere distinctly bicolorous, basally dark and concolorous with other antennomeres, apically pale yellow-white].....16

15' Pedicel shorter, robust, clavate, little less than twice length of third antennomere; corium with some hyaline cells.....17

16 (15) Antennae bifasciate, apex of pedicel and apical half of third antennomere yellow-white; pronotum wide near middle; female with apex of genital segment (=eighth connexival segment) convex, evenly rounded .....*Aradus abbas*

16' Antennae unifasciate, only apical third of third antennomere yellow-white; pronotum widest distinctly behind middle; female with apex of genital segment (=eighth connexival segment) slightly concave, angulate ..... *Aradus uniannulatus*

17 (15') Pedicel strongly narrowed in basal third; antennae blackish; third antennomere occasionally bicolorous, basally dark and concolorous with pedicel, apically yellow-white ..... *Aradus lugubris*

17' Pedicel gradually thickened from base to apex; antennae pale brownish or reddish; third antennomere concolorous with adjacent segments 18

18 (17') Antennae pale brown; head and pronotum blackish ..... *Aradus falleni*

18' Antennae testaceous; head and anterior pronotal lobe reddish ..... *Aradus subruficeps*

19 (14') Margins of pronotum entire, at most, evenly granulate 20

19' Anterolateral margins of pronotum distinctly serrate, denticulate, or tuberculate; [pronotal margins, excluding teeth, more-or-less convex, never distinctly sinuate] 22

20 (19) Third antennomere wholly pale yellow; lateral pronotal margins evenly convex; [pronotum widest before middle] ..... *Aradus uniformis*

20' Third antennomere dark; lateral pronotal margins more-or-less sinuate in anterior half.....21

21 (20') Pedicel evenly cylindrical; apex of median process of head with width subequal to average width of pedicel; pronotum widest distinctly behind middle ..... *Aradus borealis*

21' Pedicel nearly capitate, distinctly swollen at apex; apex of median process of head with width thicker than average width of pedicel; pronotum widest at middle ..... *Aradus tuberculifer*

22 (19') Pedicel approximately one-third longer than third antennomere; anterolateral angle of pronotum with robust, angular projection .....*Aradus montanus*

22' Pedical at least twice as long as third antennomere; anterolateral angle of pronotum denticulate, but without robust, angular projection.....23

23 (22') Pedicel approximately 2–2.5 times as long as third antennomere 24

23' Pedicel approximately three or more times longer than third antennomere.....26

24 (22") Pedicel shorter, subequal to interocular distance, approximately twice as long as third antennomere; third antennomere often mostly pale yellow, contrasting dark adjacent segments ..... *Aradus similis*

24' Pedicel longer, at least subequal to interocular distance + one eye, approximately 2.2–2.5 times as long as third antennomere; third antennomere concolorous with adjacent segments 25

25 (24') Pedicel slender, evenly cylindrical, not gradually thickening (except sometimes inconspicuously so at extreme apex); apex of median process of head with width easily twice apical width of pedicel; pronotal margins denticulate, teeth smaller, less conspicuous; body, in large part, pale testaceous or rufous ..... *Aradus proboscideus*

25' Pedicel more robust, gradually thickened to apex; apex of median process of head with width less than twice apical width of pedicel; pronotal margins serrate, teeth large, conspicuous; body wholly black, except posterolateral angles of connexival segments and membranous portions of wings .....*Aradus shermani*

26 (23') Abdominal tergites mesad connexiva with distinct silvery granular spots; length of pedicel subequal to three times third anntenomere..... *Aradus acutus*

26' Abdominal tergites mesad connexiva lacking silvery spots; length of pedicel distinctly greater than three times third antennomere 27

27 (26') Pedicel cylindrical from base to middle, strongly and abruptly swollen and black in apical third; lateral pronotal margins less evenly convex, appearing widest slightly behind middle ..... *Aradus approximatus*

27' Pedicel evenly enlarged from near base to apex, generally unicolorous; lateral pronotal margins more evenly convex, appearing widest at or slightly before middle ..... *Aradus inornatus*

Subfamily ANEURINAE Douglas and Scott, 1865

Genus ANEURUS Curtis, 1825

Subgenus ANEURUS Curtis, 1825

Aneurus fiskei Heidemann, 1904a. (Figs. 2, 5). – This species was reported from Michigan by Hussey (1922); he reported it "[r]ather common under the bark of the dead beeches in the Warren Woods, but found only on fallen trees." Kormilev (1968) and Picchi (1977) keyed the species of *Aneurus* found in the United States. 6 specimens examined. Collection dates from 28 May to 20 July.

Aneurus inconstans Uhler, 1871. (Figs. 2, 6). – This species was reported from Michigan by Picchi (1977); this record apparently was overlooked by Froeschner (1988). This species has been collected from "under bark" in Berrien County, from "under bark of dead limbs" in Clinton County, and from "under bark of fallen tree branch in woods" in Oakland County. It also has been collected from rotary traps both at ground level and at 12 foot height in Saginaw County. Torre-Bueno (1935) discussed the biology of this species in New York. Kormilev (1968) and Picchi (1977) keyed the species of *Aneurus* found in the United States. 54 specimens examined. Collection dates from 1 April to 30 August.

Subfamily ARADINAE Spinola, 1837

Genus ARADUS Fabricius, 1803

Aradus abbas Bergroth, 1889. (Figs. 3, 7). – This species was recorded from Michigan by Adams (1909). This species also has been collected on Isle Royale (Keweenaw County). I also examined 2 individuals of *A. abbas* with an "Ag. Coll. Mich." label, although these were excluded from the count (see *Quilnus heidemanni* Bergroth); if Michiganian, the earliest collection date to would be pushed up to 21 April. 4 specimens examined. Collection dates from 21 June to 28 August.

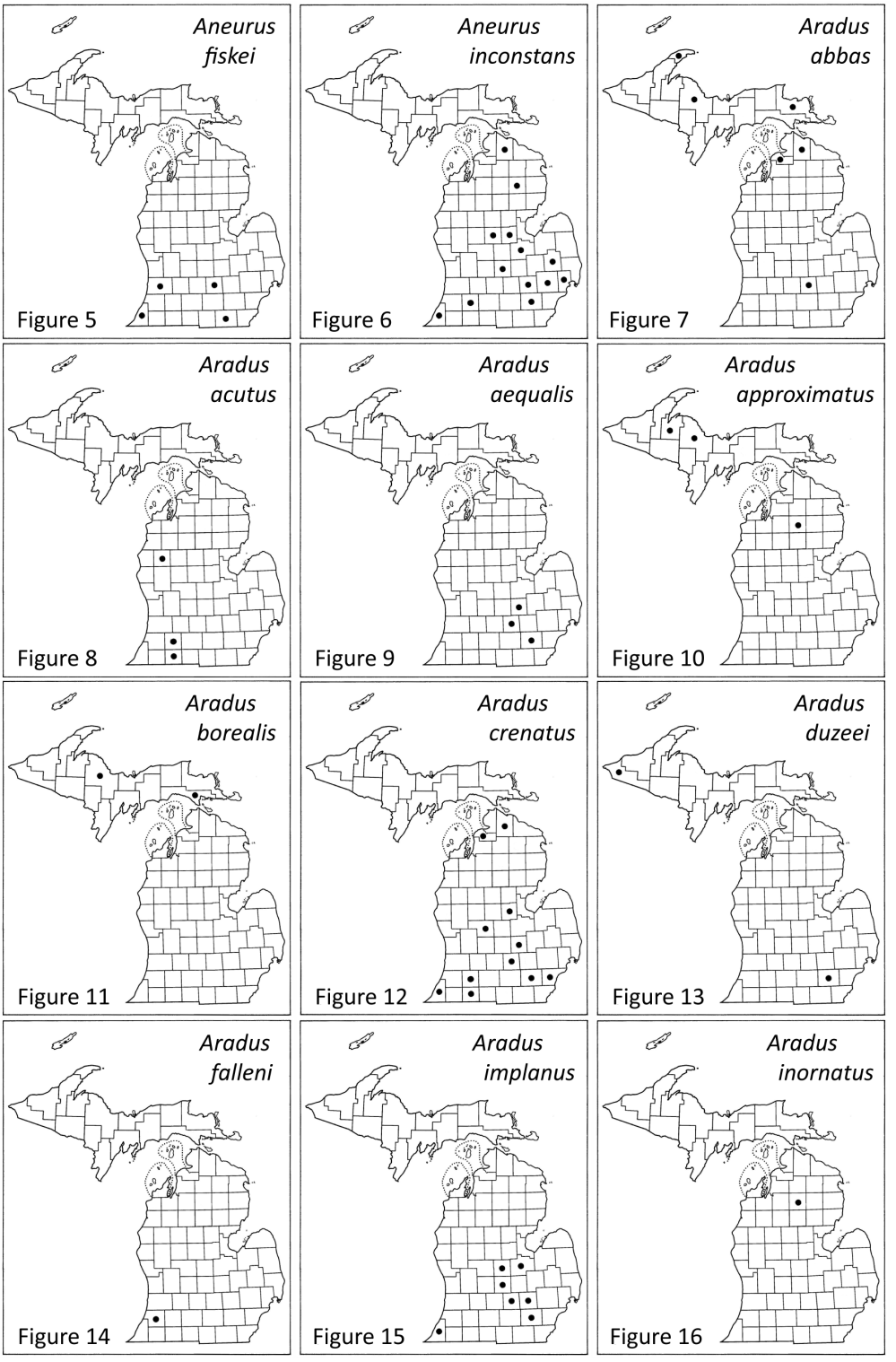
Aradus acutus Say, 1831. (Figs. 3, 8). – This species was reported from Michigan by Townsend (1890); this record apparently was overlooked by Froeschner (1988). This species has been "taken from beneath dead logs" in Kalamazoo County. In the eastern United States, *A. acutus* is easily recognized by the silvery dorsal patches mesad of the connexiva. 5 specimens examined. Collection dates from 12 July to 25 November.

Aradus aequalis Say, 1831. (Figs. 3, 9). – This species was reported only recently from Michigan by Scudder (2012). I have examined the following corroborative material: [Ingham Co.], E. Lansing, 1 May 1951, [no collector], det. D. R. Swanson 2012 [1 ♂] (MSUC); [Ingham Co.], E. Lansing, 3 May 1955, R. L. Fischer, det. D. R. Swanson 2012 [2 ♂] (MSUC); Shiawassee [Co.], 4.5 mi. NW. Perry, ex: Malaise trap, 19 June–4 July 1980, Ralph Gorton, det. D. R. Swanson 2012 [1 ♂] (MSUC); Washtenaw Co., Ann Arbor, Nichols Arboretum, 10 May 2007, 42.2806°N 83.7266°W, 870 ft., D. R. Swanson, #23, det. D. R. Swanson 2009 [1 ♀] (DRS). This species has been collected in a Malaise trap in Shiawassee County. This is one of two species of *Aradus* easily distinguished by the second and third antennomeres being subequal in length. 5 specimens examined. Collection dates from 1 May to 4 July.

Aradus approximatus Parshley, 1921. (Figs. 3, 10). – (**NEW STATE RECORD**). Label data as follows: Baraga Co., 12 July 1966, on jack pine log, W. Mattson, det. D. R. Swanson 2017 [1 ♀] (MSUC); Crawford Co., Frederic, 21 May 1965, collector R. W. Hodges, det. D. R. Swanson 2012 [1 ind., abdomen missing] (MSUC); Marquette Co., Van Riper State Park, 12–14 July 1972, D. K. & D. C. Young, det. D. R. Swanson 2012 [1 ♂] (MSUC). The species was previously known from Georgia, Indiana, Maine, Mississippi, New Jersey, and New York, as well as British Columbia, Manitoba, and Quebec (Froeschner 1988, Maw et al. 2000); thus, it was expected for Michigan. 3 specimens examined. Collection dates from 21 May to 14 July.

Aradus borealis Heidemann, 1909. (Figs. 3, 11). – This species was reported from Michigan in the original description by Heidemann (1909). An additional specimen with the following label data was examined: MICHIGAN: Mackinac Co., St. Helena Is., 26 May 1922, "472", S. Moore, det. R. F. Hussey 1950 [1 ♀] (UMMZ). 1 specimen examined. Collection dates from 26 May to 26 June.

Aradus crenatus Say, 1831. (Figs. 3, 12). – This species was reported from Michigan by Townsend (1890). This species was taken "under loose bark of a dead aspen" in Cheboygan County and "in field grass" in Wayne County, and nymphs have been "taken from rotting wood" in Shiawassee County. Usinger and Matsuda (1959, Table 1) listed several species of polypore mushroom as hosts (i.e., *Trametes versicolor* [L.] Lloyd;



Figures 5–16. Distribution of various aradid species in Michigan.

Trametes gibbosa [Pers.] Fr.; *Spongipellis unicolor* [Schwein.] Murrill). Taylor and McPherson (1989) reported this species taken from two species of fungi (i.e., *Polyporus caesius* (Schrad.) Fr.; *Bjerkandera adusta* (Willd.) P.Karst.) in Arkansas. Jordan (1932) described the morphology and development of this species. This is one of two species of *Aradus* easily distinguished by the second and third antennomeres being subequal in length. 13 specimens examined. Collection dates from 19 March to 1 October.

Aradus duzeei Bergroth, 1892. (Figs. 3, 13). – (**NEW STATE RECORD**). Label data as follows: Washtenaw Co., 6 Mile Woods, 19 May 1931, [no collector], det. R. F. Hussey 1950, det. D. R. Swanson 2012 [1 ♀] (UMMZ); Gogebic Co., 4.8 mi. N. Watersmeet, 22 June 1973, I. J. Cantrall, det. D. R. Swanson 2012 [1 ♀] (UMMZ). The species was previously known from Indiana, Massachusetts, Maryland, Missouri, New Jersey, New York, Ohio, Pennsylvania, and Virginia, as well as Ontario and Quebec (Froeschner 1988, Maw et al. 2000); thus, it was expected for Michigan. 2 specimens examined. Collection dates from 19 May to 22 June.

Aradus falleni Stål, 1860. (Figs. 3, 14). – (**NEW STATE RECORD**). Label data as follows: [Van Buren Co.], S[outh] Haven, 1 June '91, [no collector], det. D. R. Swanson 2012 [1 ind.] (MSUC). The abdomen posterior to the apex of the scutellum is ripped off. Nevertheless, the specimen remains identifiable as the head, antennae, and pronotum remain intact. One of the widest ranging species in the Western Hemisphere, *A. falleni* was previously known from Illinois and Indiana and ranges as far north as British Columbia (Froeschner 1988); thus, it was unsurprising, if not expected, to find *A. falleni* in Michigan. 1 specimen examined. Collection date is 1 June.

Aradus implanus Parshley, 1921. (Figs. 3, 15). – This species was reported from Michigan by Parshley (1921). Hussey (1922) reported it from "under the bark of a dead elm just within the Warren Woods." This species has been collected from a rotary trap in Saginaw County. 11 specimens examined. Collection dates from 23 April to 1 July.

Aradus inornatus Uhler, 1876. (Figs. 3, 16). – This species was recorded from Michigan by Parshley (1921) from "Lake Superior" with no further details. 4 specimens examined. Collection date is 21 May.

Aradus insolitus Van Duzee, 1916. (Figs. 3, 17). – (**NEW STATE RECORD**). Label data as follows: Livingston Co., E. S. George Reserve, "High Heaven", "ex: *Populus grandidentata*; standing, 6" DBH", 12 October 1979, L. Kirkendall, det. D. R. Swanson 2012 [1 ♂] (UMMZ); Oakland Co., Highland, Highland State Rec. Area, on side of wooden shed, 14 May 2011, 42.6427°N 83.5536°W, 870 ft., D. R. Swanson, #11, det. D. R. Swanson 2012 [1 ♂] (DRS). Primarily known from the western North America, i.e., Alberta, British Columbia, California, Idaho, and Oregon (Froeschner 1988), this species was not expected for Michigan. However, Maw et al. (2000) added a citation for Ontario, thereby lending support for the presence of *A. insolitus* in the eastern part of North America. The large temporal separation of the two specimens examined suggest that the species has simply gone undetected in the state. Usinger and Matsuda (1959, Table 1) listed *A. insolitus* from false turkey tail fungus (*Stereum hirsutum* [Willd.] Pers.) on quaking aspen (*Populus tremuloides* Michx.). 2 specimens examined. Collection dates from 14 May to 12 October.

Aradus intectus Parshley, 1921. (Figs. 3, 18). – (**NEW STATE RECORD**). Label data as follows: Mackinac Co., Penny Island, 26 July 1926, S. Moore, det. D. R. Swanson 2012 [1 ♀] (UMMZ); St. Clair Co., Port Huron, 1 June 1924, S. Moore, det. D. R. Swanson 2012 [1 ♀] (UMMZ). Like the previous record, this species is a primarily western element in the North American fauna, being previously known from Alberta, British Columbia, Colorado, Manitoba, Montana, Saskatchewan, Wyoming, and the Yukon Territories (Froeschner 1988, Maw et al. 2000). Thus, it was not expected for Michigan. However, the robustness of the antennae (in relation to the profemora) set it apart from the majority of other species of *Aradus* found in the state. 2 specimens examined. Collection dates from 1 June to 26 July.

Aradus lugubris Fallén, 1807. (Figs. 4, 19). – This species was reported from Michigan by Townsend (1890) (as *Aradus rectus* Say, 1831). This species has been collected on Isle Royale (Keweenaw County). I also examined 8 individuals of this species with an "Ag. Coll. Mich." label, although these were excluded from the count (see *Quilnus heidemanni*). Currently all Michigan records would be assigned to the nominate subspecies; however, *Aradus lugubris nigricornis* Reuter, 1900, might also be found in the state, being known from Alaska, Arizona, California, Colorado, Idaho, Maine, Massachusetts, Nevada, New Mexico, Oregon, Washington, and Wisconsin, as well as British Columbia, Northwest Territories, and Ontario (Froeschner 1988). They are separated by *A. l. nigricornis* possessing wholly black antennae, whereas those in the nominate subspecies have the apex of the third antennomere, and occasionally that of the pedicel, white. However, Parshley

(1921) noted that *A. l. lugubris* "exhibits intergradational variation in the amount of white on the antennae", concluding that "[i]t is not of geographical significance." 6 specimens examined. Collection dates from 21 April to 30 August.

Aradus montanus Bergroth, 1913. (Figs. 4, 20). – (**NEW STATE RECORD**). Label data as follows: Mackinac Co., St. Helena Island, 26 May 1922, S. Moore, det. R. F. Hussey 1950, det. D. R. Swanson 2012 [1 ♀] (UMMZ). This species was previously known from Colorado, Montana, and Quebec; thus, it is plausible, if not expected, to find this species in Michigan. However, as indicated in the key, this species is distinctive among species with serrate pronotal margins in its short pedicel. 1 specimen examined. Collection date is 26 May.

Aradus proboscideus Walker, 1873. (Figs. 4, 21). – (**NEW STATE RECORD**). Label data as follows: Cheboygan Co., Cheboygan, 12 May 1921, "333", S. Moore, det. R. F. Hussey 1921, [1 ♀] (UMMZ); Keweenaw Co., Isle Royale, N.P., 3-mile camp, 2 September 1975, J. K. Liebherr, det. D. R. Swanson 2012 [1 ♂] (MSUC). This species was previously known from Manitoba, Ontario, Quebec, south to Wyoming, Colorado, and New York (Froeschner 1988, Maw et al. 2000); thus, it is plausible for this species to be found in Michigan. Usinger and Matsuda (1959, Table 1) listed *A. proboscideus* from red-belt conk fungus (*Fomitopsis pinicola* [Swartz ex Fries] P.Karst.), and "spruce fungus". 2 specimens examined. Collection dates from 12 May to 2 September.

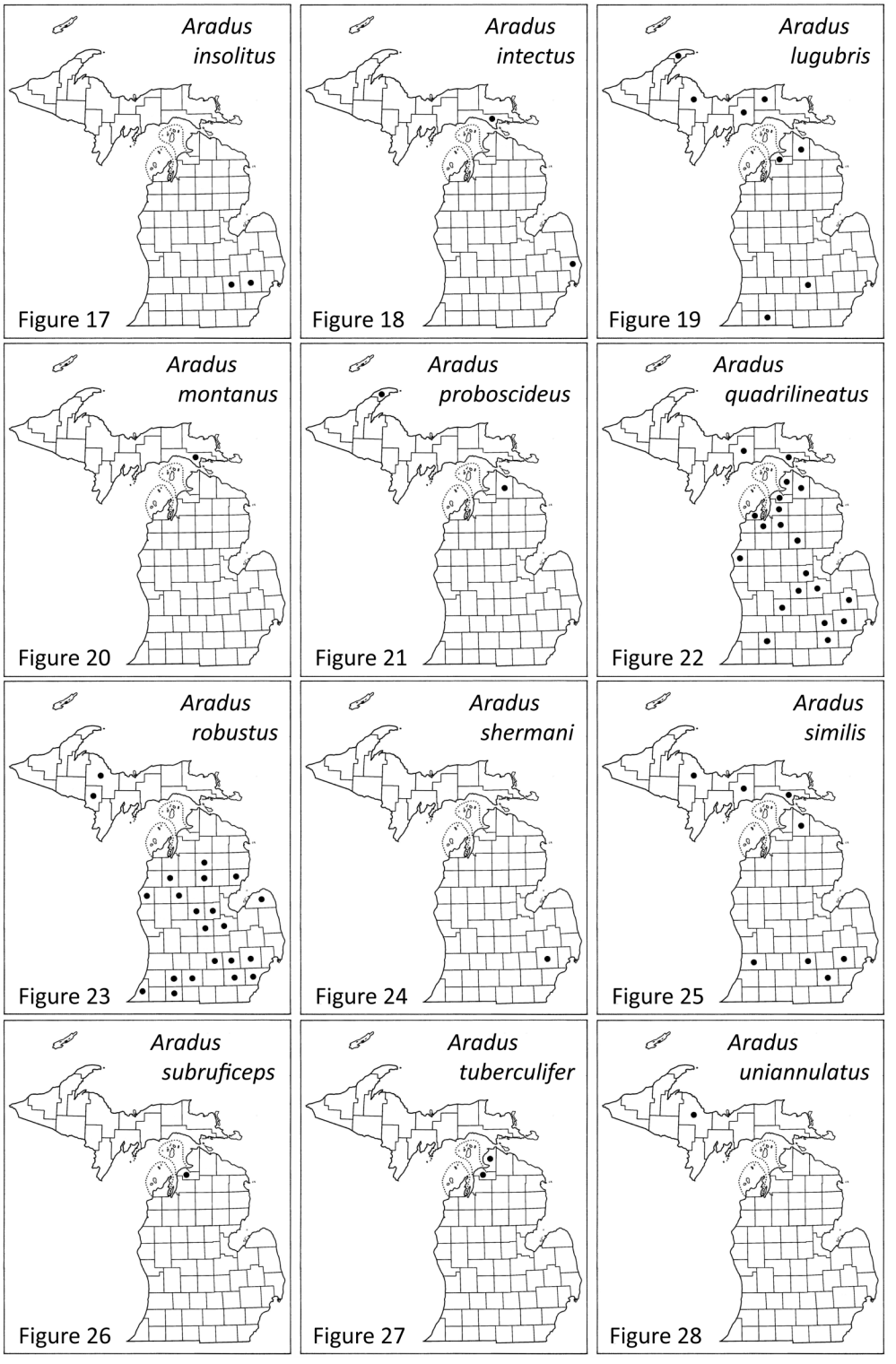
Aradus quadrilineatus Say, 1825. (Figs. 4, 22). – This species was recorded from Michigan by Parshley (1921). The species has been collected from "under bark of oak stump" in Washtenaw County. This species has been collected on St. Helena Island (Mackinac County). Barber (1923) described the natural history and various life stages, notably the egg, of this species. Torre-Bueno (1935) discussed the biology of this species in New York. This common species is unique and instantly recognizable by the configuration of the antennae. 41 specimens examined. Collection dates from 23 April to 11 August.

Aradus robustus Uhler, 1871. (Figs. 4, 23). – This species was reported from Michigan by Townsend (1890) and Parshley (1921). Hussey (1922) reported it "from the bark of a large fallen beech in the flood-plain forest in the Warren Woods." This species has been collected in a Malaise trap in Dickinson County, in a pitfall trap in Ingham County, from rotaries traps, some at ground level, in Saginaw County, and "sweeping" in Washtenaw County. Leschen and Taylor (1987) and Taylor and McPherson (1989) reported this species taken from the white-rot fungus *Irpex lacteus* (Fr.) Fr. Torre-Bueno (1935) discussed the biology of this species in New York, and Leschen and Taylor (1987) discussed aspects of the biology and distribution in several eastern states. Although I have examined two individuals that could be referred to the subspecies *Aradus robustus insignis* Parshley, 1921, a subspecies recorded from Michigan in the original description, I have declined to include separate divisions for the two subspecies. Parshley (1921) noted that *A. r. insignis* was a color variant of "no geographical significance." The two are separated by portions of the yellowish portions of the pronotum, scutellum and corium, as well as the reddish dorsal coloration of the abdomen, in *A. r. insignis,* as opposed to the uniformly dark coloration in the nominate subspecies. 49 specimens examined. Collection dates from 12 April to 20 July.

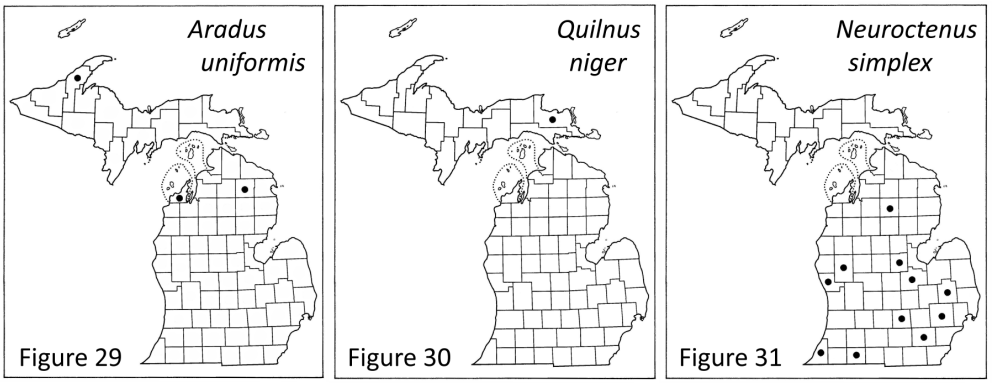
Aradus shermani Heidemann, 1906. (Figs. 4, 24). – (**NEW STATE RECORD**). Label data as follows: Oakland Co., Milford, 22 June 1921, "35", T. H. Hubbell, det. R. F. Hussey 1921 [1 ♂] (UMMZ). This species was previously known from Alabama, Florida, Georgia, Maine, New Jersey, North Carolina, Ontario, Pennsylvania, Quebec, Saskatchewan, and the Yukon Territories (Froeschner 1988, Maw et al. 2000); thus, it is plausible for this species to be found in Michigan. 1 specimen examined. Collection date is 22 June.

Aradus similis Say, 1831. (Figs. 4, 25). – This species was recorded from Michigan by Parshley (1921). I also examined 1 individual of this species with an "Ag. Coll. Mich." label, although this was excluded from the count (see *Quilnus heidemanni*); if Michiganian, the earliest collection date to would be pushed up to 6 May. Usinger and Matsuda (1959, Table 1) listed this species from *Polyporus* fungus on birch (*Betula* sp.). 9 specimens examined. Collection dates from 12 May to 18 August.

Aradus subruficeps Hussey, 1953. (Figs. 4, 26). – This species was described from Michigan by Hussey (1953) based on a single individual. It remains possible that *A. subruficeps* is merely a teneral individual of *A. falleni*, and Hussey (1953) noted that it runs to that species in various keys. However, he stated "It agrees in size with smaller individuals of that species, but is at once distinct by reason of its color, the very different proportions of head and pronotum, the nonfenestrate ventral genital segment of the male, and so forth." Thus, it is retained here as a valid species. 1 specimen (holotype) examined. Collection date is 31 July.



Figures 17–28. Distribution of various aradid species in Michigan.



Figures 29–31. Distribution of various aradid species in Michigan.

Aradus tuberculifer Kirby, 1837. (Figs. 4, 27). – This species was recorded from Michigan (without any locality information) by Parshley (1921). I examined the following two corroborative specimens: Charlevoix Co., Whiskey Is., 9 June 1923, "589", S. Moore, det. R. F. Hussey 1950 [1 ♂] (UMMZ); Emmet Co., Waugoshance Pt., 22 May 1922, "470", S. Moore, det. R. F. Hussey 1950 [1 ♂] (UMMZ). 2 specimens examined. Collection dates from 22 May to 9 June.

Aradus uniannulatus Parshley, 1921. (Figs. 4, 28). – This species was recorded from Michigan by Parshley (1921). At the time, the single Michiganian paratype was retained in Parshley's collection, and it currently resides in the California Academy of Sciences (CAS) (Zuparko, pers. comm., 2016). No specimens examined. Collection date is 28 August.

Aradus uniformis Heidemann, 1904b. (Figs. 4, 29). – (**NEW STATE RECORD**). Label data as follows: Leelanau Co., South Fox Island, 27 May 1925, S. Moore, det. R. F. Hussey 1950, det. D. R. Swanson 2012 [2 ♀] (UMMZ); Montmorency Co., 6 mi. N. Atlanta, Jackson Lake Forest Campground, 22 June 1995, M. A. & M. O'Brien, det. D. R. Swanson 2012 [1 ♀] (UMMZ). This aradid also has been collected from Isle Royale (Keweenaw County). This species was previously known from Florida, Massachusetts, Maryland, New Jersey, New York, North Carolina, Pennsylvania, and Virginia, as well as Ontario (Froeschner 1988); thus, it was expected for Michigan. 4 specimens examined. Collection dates from 27 May to 22 June.

Genus QUILNUS Stål, 1873

Quilnus heidemanni (Bergroth, 1906). – I have examined a single female of *Q. heidemanni* in MSUC. It bears the following label data: "Ag. Coll. Mich., 3-21-'90, 14, det. D. R. Swanson 2012". This specimen, however, is excluded, because labels of this type typically denote ownership rather than a collecting locality (O'Brien 1998). It is primarily a western species, being known from California, Colorado, Montana, New Mexico, Oregon, and Washington, as well as Alberta and British Columbia (Froeschner 1988). Given these factors, it seems prudent to exclude this species from Michigan's faunal list at this time.

Quilnus niger (Stål, 1873). (Fig. 4, 30). – (**NEW STATE RECORD**). Label data as follows: Chippewa Co., 27 August 1941, R. R. Dreisbach, det. D. R. Swanson 2012 [1 micropterous ♀] (MSUC). This species, being known from Missouri, New York, Ontario, and Quebec, among other states and provinces (Froeschner 1988), was expected for Michigan. Heidemann (1901) discussed the habitats of this species. 1 specimen examined. Collection date is 27 August.

Subfamily MEZIRINAE Oshanin, 1910

Genus MEZIRA Amyot and Audinet-Serville, 1843

Mezira lobata (Say, 1831). (Fig. 2). – This species was recorded from Michigan by Uhler (1876) and Blatchley (1926), although neither provided specific localities in the state. Froeschner (1988) listed "Canada", in addition to Midwestern states, such as Illinois, Indiana, and Ohio; thus, it seems plausible for the species to be found in Michigan, assuming records from Canada are valid. Furthermore, being one of the "large" species of *Mezira*, it should be easily distinguished from the other mezirine species known from the state. Usinger (1936) and Kormilev

(1962, 1971) keyed the genus. No specimens examined. Collection date unknown.

Genus NEUROCTENUS Fieber, 1860

Neuroctenus simplex (Uhler, 1876). (Fig. 2, 31). – (**NEW STATE RECORD**). Given the number of specimens examined, it remains surprising that this species was heretofore unreported from Michigan. Certainly, its presence in Michigan was plausible, as it was previously known from Illinois, Maine, Montana, and Ohio, among other states (Froeschner 1988), and this dearth of records might come from the occasional difficulty in separating *N. simplex* from its congeners, as well as similar-sized, i.e., "small", species of *Mezira*. This species has been taken "under hickory or oak bark" and "taken on *Quercus velutina*" in Washtenaw County. I also examined 25 individuals of this species with an "Ag. Coll. Mich." label, although these were excluded from the count (see *Quilnus heidemanni*). Kormilev (1982a) keyed the genus. 52 specimens examined. Collection dates from 13 February to 14 November.

NOTES ON ADDITIONAL SPECIES

The cryptic characteristics of aradids likely contribute to an underestimation of the biodiversity in the state. These cryptic facets of aradids also suggest that the distribution of many aradid species is poorly-understood. As highlighted above, the presence of several predominantly western elements in Michigan contributes further evidence toward this incomplete understanding regarding aradid ranges. Therefore, mention of species that might eventually be found in Michigan is warranted. In this context, there are three tiers of species' ranges to consider. First, four species are known from across portions of Canada but also in the northern corners of the United States, thereby including Michigan in the potential range on strictly latitudinal criteria: *Aneurus borealis* Picchi, 1977; *Aradus debilis* Uhler, 1876; *Aradus funestus* Bergroth, 1913; and *Aradus persimilis* Van Duzee, 1916. The sole member of the second tier is *Aradus paganicus* Parshley, 1929, being known from both eastern and western Canada, specifically British Columbia and Ontario, but not yet known from the United States. The third tier encompasses six species, all but one being mezirines, that are present in adjacent states to the south, and therefore might be found in southern Michigan: *Aradus ornatus* Say, 1831; *Mezira granulata* (Say, 1831); *Mezira sayi* Kormilev, 1982b; *Nannium pusio* Heidemann, 1909; *Neuroctenus elongatus* Osborn, 1903; and *Neuroctenus pseudonymus* Bergroth, 1898. It is important to keep these potential additions in mind when keying out specimens. These species are not included in the key, and more inclusive treatments, particularly those of more boreal species such as Matsuda's (1977) *Aradidae of Canada*, should be consulted. Two species bear special consideration:

Aneurus simplex Uhler, 1871. – Although the currently known range is similar to that of "tier 1 species" mentioned above, *A. simplex* is found farther south in several portions of its range. Distributed widely across Canada (Alberta, British Columbia, Manitoba, Newfoundland and Labrador, Northwest Territories, Nova Scotia, Ontario, Quebec, and Yukon Territories), this species also occurs in Alaska, Colorado, Idaho, Maine, Massachusetts, Montana, New Hampshire, New Jersey, New York, North Carolina, Oregon, Vermont, Washington, and Wyoming (Froeschner 1988, Maw et al. 2000). Usinger and Matsuda (1959, Table 1) listed Sitka spruce (*Picea sitchensis* [Bong.] Carr.) as a host record for this species, although this species of spruce is not found in Michigan (Barnes and Wagner 2004). Like *A. inconstans*, the pedicel is more similar to the third antennomere than the scape; however, *A. simplex* is unique from all species of *Aneurus* known from the United States in the lateral (visible in dorsal view), rather than ventral, spiracle of the fifth abdominal tergite.

Aradus kormilevi Heiss, 1980. – Previously confounded with the pestiferous *Aradus cinnamomeus*, *A. kormilevi* will surely be found in Michigan. Having been recorded from Alabama, California, Colorado, Florida, Georgia, Kansas, Maryland, Massachusetts, Mississippi, Missouri, Montana, Nebraska, New Jersey, Pennsylvania, Texas, Virginia, West Virginia and Wyoming, as well as Washington, D.C. and Alberta, British Columbia, Manitoba, New Brunswick, Nova Scotia, Ontario, Quebec, and Saskatchewan (Froeschner 1988, Maw et al. 2000), the current known range of this species encloses Michigan. Despite belonging to the same complex as *A. cinnamomeus*, this species is not known to be economically impactful (Heliövaara 2000). Usinger and Matsuda (1959, Table 1) listed many host records for *A. cinnamomeus*, of which the following trees are found in Michigan (Barnes and Wagner 2004): Scots pine (*Pinus sylvestris* L.), black pine (*Pinus nigra* Arnold), jack pine (*Pinus banksiana* Lamb.), white fur (*Abies concolor* [Gordon and Glend.] Lindley ex Hildebrand), Norway spruce (*Picea abies* [L. H.Karst.]), common alder (*Alnus glutinosa* [L.] Gaertn.), juniper (*Juniperus* sp.), and willow (*Salix* sp.). However, these records might be either shared or confounded with *A. kormilevi*. The species is easily recognized from other

aradines by the obliterated pronotal carinae, the short moniliform antennae, the wide "snout", small body size (less than 4 mm), and reddish-brown coloration. This is the only species in the United States known to have stenopterous morphs.

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New State Records for Some Flat Bugs (Heteroptera: Aradidae) of the United States

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Abstract

Twelve new state records are reported for eleven previously described species in six genera of Aradidae found in the United States.

Keywords: Hemiptera, true bugs, faunistics, distribution, Nearctic

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As a companion piece to my Michigan Aradidae synopsis (i.e., Swanson 2020), I have re-examined and identified the Aradidae in the two major collections in southern Michigan in order to bring to light unreported state records. As a result, 12 new extra-Michigan state records, comprising material from the Michigan State University Albert J. Cook Arthropod Research Collection in East Lansing, the University of Michigan Museum of Zoology Insect Collection in Ann Arbor, and my personal collection, are herein reported.

Materials and Methods

Methodology largely follows my previous treatments (i.e., Swanson 2011, 2018, 2019):

After examining the determined aradid holdings and identifying much of the undetermined U.S. material in two Michigan university collections, the locality data of these specimens were compared with the most recent catalog for Heteroptera found north of Mexico (Henry and Froeschner 1988). Further records were culled after comparing with various post-1988 regional faunistic studies, as well as some pre-1988 references overlooked by the authors of the catalog (see annotations, plus Swanson 2011, 2018, 2019). The remaining specimen data are the subject of this treatment.

The identification of all specimens included in this study was rendered or confirmed by me, using my own keys (Swanson, unpublished) to the United States taxa synthesized from various sources (e.g., Parshley 1921, Blatchley 1926, Torre-Bueno 1939, Matsuda 1977). In most cases, I have confirmed identifications previously rendered by R. F. Hussey.

Label data were not copied verbatim, although complete locality information is included. Any additions, changes, or interpretive elements I provide are shown in brackets. Multiple localities are included, where possible, to fortify new records. Distributional or taxonomic notes are offered where deemed necessary or useful.

As mentioned, the authority on which a state having a published record for a given aradid species is based belongs to Froeschner (1988). An updated distribution within the United States and Canada is included for each species treated herein. Records overlooked or reported subsequently are annotated in the distribution north of Mexico given at the end of each species account, whereas new records herein reported are presented in bold type; thus, this treatment also may be used as a partial compilation of references overlooked in Henry and Froeschner's (1988) catalog. The abbreviations used for each U.S. state and Canadian province or territory follow the United States Postal Service and the Canada Post Corporation, respectively.

Collections are designated as follows: Daniel R. Swanson, personal collection (DRS); Albert J. Cook Arthropod Research Collection, Michigan State University, East Lansing, Michigan (MSUC); and University of Michigan Museum of Zoology Insect Collection, Ann Arbor, Michigan (UMMZ).

Results

As a result of this investigation, 12 new state records for 11 previously described species in 6 genera have been compiled. The following 8 states have new records: IL, KY, LA, MO, TN, VA, WI, WY.

Subfamily ANEURINAE

Aneurus inconstans Uhler, 1871. – **TENNESSEE**: Carter Co., Roan Mountain, elevation 6300 ft., 6 August 1922, T. H. Hubbell, det. D. R. Swanson 2012 [1 ♂, 1 ♀] (UMMZ).

Distribution: USA: CT, DC, DE, IN, MA, MD, ME, MI (Swanson 2020), NC, NH, NJ, NY, OH (Osborn and Drake 1915), PA, RI, SD, **TN**, VA, VT; Canada: AB, BC, MB (Maw et al. 2000), NS, ON, QC, SK (Maw et al. 2000).

Iralunelus politus (Say, 1831). – **LOUISIANA**: Orleans Co. [sic], New Orleans, 24 February 1923, T. H. Hubbell, det R. F. Hussey 1950 [4 ♀, 2 nymphs] (UMMZ).

Notes: Kormilev and Froeschner (1987) raised the subgenus *Iralunelus* Štys, 1974 to full generic rank, at the same time treating *Aneurus leptocerus* Hussey, 1957 and *Aneurus politus* Say, 1831 in combination with *Iralunelus*. It is unknown to me why these changes were not incorporated in the Henry and Froeschner's (1988) catalog. Štys (1974), in erecting *Iralunelus*, treated Say's species as *Aneurus* (*Iralunelus*) *politus*, but Froeschner (1988), despite co-authoring the new combinations, oddly noted for *Aneurus* Curtis, 1825: "Four subgenera have been placed within this genus…All species in the area north of Mexico appear to belong to the nominate subgenus."

Distribution: USA: AL, FL, GA, **LA**, MS, NY.

Subfamily ARADINAE

Aradus cincticornis Bergroth, 1906. – **ILLINOIS**: Will Co., Crete, 8 April 1906, H. Rumstadt, *Aradus proboscideus* Walker det. R. F. Hussey 1950, *Aradus cincticornis* Bergroth det. D. R. Swanson 2018 [1 ♀] (UMMZ).

Notes: Hussey originally identified this specimen as *Aradus proboscideus* Walker, 1873. However, in *A. proboscideus*, the disc of the pronotum is more or less flat, not being raised in front or behind the rather shallow transverse sulcus, whereas *A. cincticornis* (and the Illinoisan specimen) has the transverse sulcus deep and the disc distinctly raised in front and behind.

The single female on which this record is based has a body length of 8.6 mm. This "breaks" couplet #26 of Parshley's (1921) key (and Blatchley's [1926] key based on it), which purports that the body length of *A. cincticornis* is less than 6.8 mm.

Distribution: USA: AL, AR (Taylor and McPherson 1989), **IL**, MO.

Aradus crenatus Say, 1831. – **KENTUCKY**: Jackson Co., 5.4 air mi. NE. McKee, Turkey Foot Camp, 27 July 2010, 37.4708°N 83.9143°W, 880 ft., D. R. Swanson, #28, det. D. R. Swanson 2012 [1 ♀] (DRS).

Distribution: USA: AL, AR (Taylor and McPherson 1989), CT, DC, GA, IL, IN, **KY**, MD, MI, MO, NC, NY, OH, PA, TN (Blöte 1965), VA; Canada: ON, QC.

Aradus lugubris Fallén, 1807. – **WYOMING**: Johnson Co., Bighorn National Forest, Tie Hack Campground, T50N, R84W, Sec. 26, 11–12 July 1974, Thomas A. Bowling, det. D. R. Swanson 2012 [1 ♀] (MSUC).

Notes: The antennae of this specimen are entirely black, aligning it with *Aradus lugubris nigricornis* Reuter, 1900. However, Parshley (1921) treated *nigricornis* as an intergradational color variety with no geographic significance, and I follow the spirit of that treatment.

Distribution: USA: AK, AZ, CA, CO, DC, IA (Osborn 1892), ID, IL, MA, ME, MI, MN, MO, MT, NC, ND, NE, NH, NM, NV, NY, OR, PA, RI, UT, WA, WI, **WY**; Canada: AB, BC, MB, NF, NS, NT, ON, QC, SK, YT.

Subfamily MEZIRINAE

Aphleboderrhis pubescens (Walker, 1873). – **MISSOURI**: Oregon Co., McCormack Lake, Shawnee National Forest, 6 June 1968, E. J. Kochenderfer, det. D. R. Swanson 2012 [1 ♀] (MSUC).

Distribution: USA: **MO**, TX.

Mezira emarginata (Say, 1831). – **TENNESSEE**: Chester Co., 9 mi. W. Henderson, [illegible] September 1972, R. D. Ward, det. D. R. Swanson 2012 [1 ♀] (MSUC).

Distribution: USA: AR, AZ, CA, FL, MS, NC, NM, NV, **TN**, TX.

Mezira granulata (Say, 1831). – **VIRGINIA**: Fairfax Co., Herndon, August 1911, [no collector?], det. H. G. Barber 1919, det. D. R. Swanson 2013 [1 ♀] (UMMZ); Fairfax Co., Springfield, 5–9 April 1976, R. D. Ward, det. D. R. Swanson 2013 [1 ♂, 4 ♀] (MSUC).

Distribution: USA: AL, AR (Taylor and McPherson 1989, Davidová-Vilímová et al. 1996), AZ, DC, FL, GA, IL (Davidová-Vilímová et al. 1996), IN, MD, MO, NC, OK (Davidová-Vilímová et al. 1996), SC, TN (Lambdin et al. 2003, Vlach et al. 2010), TX, **VA**.

Mezira sayi Kormilev, 1982. – **TENNESSEE**: Chester Co., Chickasaw State Park, 9 July 1974, R. D. Ward, det. D. R. Swanson 2013 [1 ♂] (MSUC); [Fentress Co.], Allardt, 20 August 1922, T. H. Hubbell, det. D. R. Swanson 2013 [3 ♂, 4 ♀, 2 nymphs] (UMMZ); Hardeman Co., Bolivar, 19 March 1974 [add. dates: 24 December 1977, 27 December 1977], R. D. Ward, det. D. R. Swanson 2013 [4 ♂, 4 ♀] (MSUC); **VIRGINIA**: Fairfax Co., Herndon, August 1911, [no collector?], det. D. R. Swanson 2013 [1 ♀] (UMMZ); Fairfax Co., Springfield, 12–14 June 1976, R. D. Ward, det. D. R. Swanson 2013 [1 ♀] (MSUC).

Note: A single female from Washington with the following locality data could not be separated from *M. sayi*: **WASHINGTON**: Whitman Co., Pullman, 21 September 1919, Phillip Putnam, det. D. R. Swanson 2012 [1 ♀] (UMMZ). However, this represents a large range disjunction, as the nearest records of *M. sayi* are from Illinois and Texas (Davidová-Vilímová et al. 1996). Thus, it is possible that this female represents an undescribed species. A passive introduction of *M. sayi* into the Pacific Northwest also remains a possibility. Given the uncertainty, I simply note its existence here, without a formal identification.

Distribution: USA: AR (Taylor and McPherson 1989, Davidová-Vilímová et al. 1996), FL, GA, IL (Davidová-Vilímová et al. 1996), IN, LA (Davidová-Vilímová et al. 1996), MS (Davidová-Vilímová et al. 1996), NC (Davidová-Vilímová et al. 1996), SC, **TN**, TX (Davidová-Vilímová et al. 1996), **VA**.

Neuroctenus simplex (Uhler, 1876). – **WISCONSIN**: Shawano Co., [no further locality data], 6 September 1950, [no collector], det. D. R. Swanson 2012 [1 ♀] (MSUC).

Distribution: USA: AR (Taylor and McPherson 1989), CT, DC, FL, GA, IA (Osborn 1898), IL, IN (Blatchley 1895, 1926), KS, MA, MD, ME, MO, MT, NC, NJ, NY, OH, OK (Ortenburger 1926), PA, SC, TX, **WI**; Canada: ON (Paiero et al. 2003).

Neuroctenus unistellatus Vásárhelyi, 1994. – **MISSOURI**: Oregon Co., McCormack Lake, Shawnee National Forest, 6 June 1968, Roland L. Fischer, det. D. R. Swanson 2018 [1 ♂] (MSUC).

Note: Although they are figured, Vásárhelyi (1994) did not draw attention to the large eighth paratergites in the male of this species, despite the form of these structures being unique among congeners north of Mexico.

Distribution: USA: **MO**, TX.

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Minnesota State Records for *Osmia georgica, Megachile inimica,* and *Megachile frugalis* (Hymenoptera, Megachilidae), Including a New Nest Description for *Megachile frugalis* Compared with Other Species in the Subgenus *Sayapis*

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Abstract

In this article, we report the first Minnesota state records of *Osmia (Helicosmia) georgica* Cresson 1878, *Megachile (Sayapis) inimica* Cresson 1872, and *Megachile (Sayapis) frugalis* Cresson 1872, which were collected in 2018. We also provide the first description of the nest structure of *M. frugalis*. All three species typically have more southern distributions. The nest of *M. frugalis* shows similar structure to other species in the subgenus *Sayapis* Titus, such as *M. inimica* and *M. pugnata* Say, particularly in that the longitudinal nest cell walls lack a lining of leaf pieces, and the cell partitions are made from a layer of leaf pieces followed by a layer of masticated vegetation and soil particles.

Keywords: *Megachile inimica*, *Megachile frugalis*, *Sayapis*, *Osmia georgica*, natural history, cavity-nesting, trap nest, solitary bees, nest architecture

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In this paper, we report the first records of *Osmia georgica* Cresson, *Megachile inimica* Cresson, and *Megachile frugalis* Cresson in the state of Minnesota. Prior to this, *O. georgica* has shown a predominantly southeastern distribution in the United States of America, with digitized records showing it present along the entire eastern coast and west through Michigan, Nebraska and Texas. Both *Megachile* Latreille species have been recorded across the southern USA, extending northwards into southern Wisconsin, Michigan, New England and south into Mexico and central America (Medler and Lussenhop 1968, Gibbs et al. 2017, GBIF.org 2020). These new records for Minnesota add to the 18 species of *Osmia* Panzer and 22 species of *Megachile* currently known from the state (MNDNR 2019). In the United States as a whole there are 140 species of *Osmia* and 138 species of Megachile (Ascher and Pickering 2020). Bees in the genera *Osmia* and *Megachile* are solitary-nesting bees that typically use vegetative matter or mud to construct nest cells, although some species do use resin (Cane et al. 2007, Michener 2007, Sheffield et al. 2011).

The two new Megachile species reported here both belong to the subgenus *Sayapis* Titus. Prior to this, Minnesota has had only a single representative of the subgenus: *Megachile pugnata* Say. Species in the subgenus *Sayapis* have unusual nest structure compared with other congeners. Among the (*Sayapis*) species found in the United States, nests have been described for *M. pugnata*, *M. inimica*, *Megachile policaris* Say, and *Megachile zaptlana* Cresson (Table 1; Mitchel 1937, Medler 1964, Krombein 1967, Medler and Lussenhop 1968, Frohlich and Parker 1983, Raw 1984, MacIvor 2016, dos Santos et al. 2020). Two others, *Megachile fidelis* Cresson and *Megachile newberryae* Cockerell, have been recorded nesting in stems or wood, but their nest structure information is lacking (Mitchell 1937, Butler 1965, Barthell et al. 1998, Frankie et al. 1998). We know of no references of nests of *Megachile mellitarsis* Cresson or *M. frugalis*.

In addition to details of these new state records, we also provide the first description of the nest structure of *M. frugalis* in comparison with *M. inimica* and published nest descriptions of other species within the

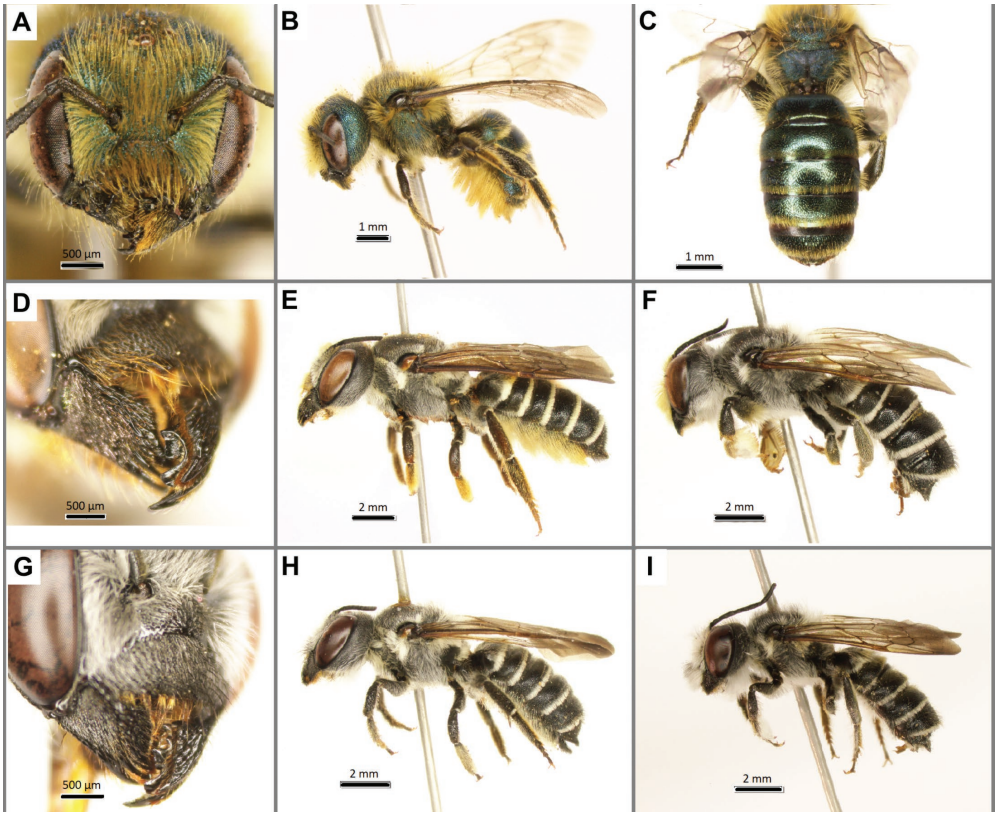

Figure 1: A) Female *O. georgica* mandible. B) *O. georgica* female side, note projection on mandible and yellow scopa. C) *O. georgica* male abdomen, note propodeal slit and T6 notch. D) *M. inimica* female mandible, note central point on clypeus. E) *M. inimica* female side. F) *M. inimica* male side, note lack of black brush on expanded forebasitarsis. G) *M. frugalis* female mandible, note black hair on clypeus. H) *M. frugalis* female side I) *M. frugalis* male side. (Photos courtesy of Thea Evans).

subgenus *Sayapis* which inhabit the United States.

Methods and Materials

Bees were collected with nest blocks as part of the citizen science project "Minnesota Bee Atlas" (https://z.umn.edu/beeatlas). Blocks were made from untreated pine or Douglas fir, with a roof of cedar shingling. Each block measured approximately 8.9 × 14 × 27.9 cm (3.5 × 5.5 × 11 in.) and contained five tunnels each of six different diameters: 3.18 mm, 4.76 mm, 6.35 mm, 7.94 mm, 9.53 mm, and 11.11 mm. Tunnels were approximately 11.43 cm (4.5 in.) deep and spaced 2.54 cm (1 in.) away from other tunnels or the block edge. Each block was identified by a unique number, and tunnels within blocks by unique letter-number combinations.

Volunteers across the state of Minnesota were selected to hang and monitor a nest block in a semi-natural habitat. In March 2018, a total of 140 nest blocks were sent out. Recommended block placement was 0.9–1.5 meters high facing south or east in a semi-sunny location. Volunteers were asked to record specific mounting conditions of their block and report every 2–3 weeks on evidence of nesting. All records discussed in this paper come from southern Minnesota. The nest block that yielded *O. georgica*, number 502, was placed in Winona County, Minnesota, southeast of the town of Lewiston (43.94986°N, –91.82164°W). According to volunteer observation, it was mounted next to several acres of Conservation Reserve Program (CRP) land containing trees, grasses, and native wildflowers, at a height of 1.22 m, facing southeast. The five *M. inimica* nests were distributed between two blocks. One block, number 453, was located near Revere in Cottonwood County (44.13895°N, –95.3601°W), and hung 1.2–1.4 m high,

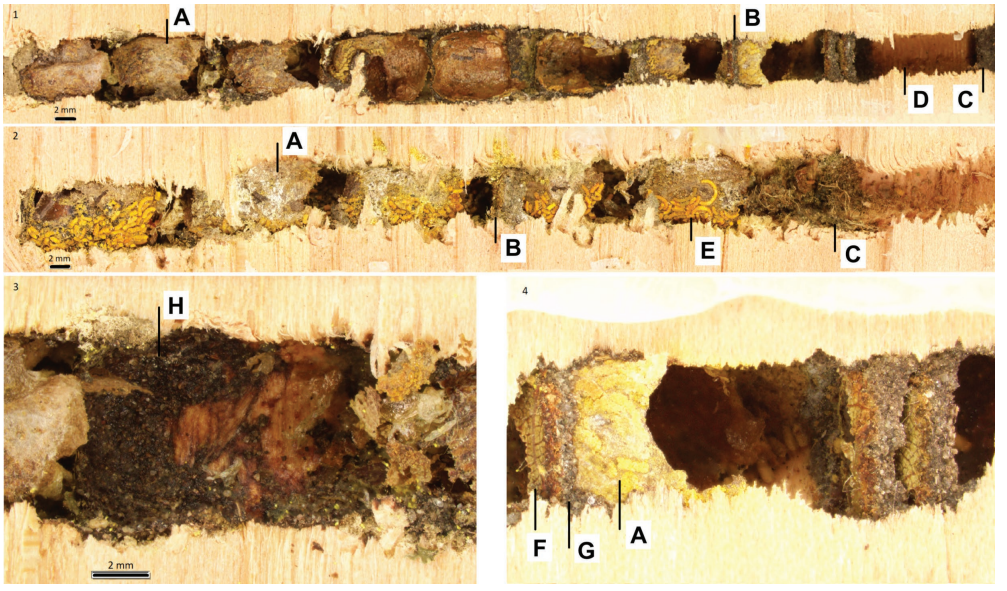

Figure 2. Nests of *M. frugalis* (top) and *M. inimica* (middle), with entrances to right, A=cocoon, B=cell partition, C=final nest plug, D=vestibule, E=frass. Bottom left: close up of 2nd cell of *M. frugalis* nest with cocoon removed - note partial lining of cell walls (H) with chewed vegetation. Bottom right: Close up of 8th cell of *M. frugalis* nest showing partition construction in more detail, F=leaf piece, G=chewed vegetation and soil particles. (Photos courtesy of Thea Evans).

facing southeast. The other block, 467, was located on the edge of Dover in Olmstead County (43.96863°N, –92.1343°W), and hung four feet high, facing south. The block was situated in a lawn with hostas, a highbush cranberry and arborvitae, very close to farmland and grassland. The block containing the *M. frugalis* nest, number 472, was located near Bingham Lake in Cottonwood County, (43.92406°N, –95.0407°W), and hung 1.37 m high, facing south. The volunteer described the location as bordering Conservation Reserve Program land with abundant flowers and near a lake.

In the late fall, blocks were returned to the University of Minnesota where they were surveyed by otoscope, overwintered and reared to emergence in a growth chamber the following year. Warming for emergence was conducted with constant temperature steps, rather than by tracking local daily fluctuations, therefore bee emergence dates suggest relative seasonality rather than actual emergence in field conditions. To capture emerging bees, a hollowed-out plastic test-tube cap was glued over each tunnel entrance and a replaceable test tube was inserted in the cap. Emerged bees in test tubes were removed daily and new tubes placed on tunnels. Bee identification was done by C. D. Satyshur using Mitchell (1962), Sandhouse (1939), and Discover Life keys (Andrus et al. 2020, Griswold et al. 2020, Nelson and Droege 2020a,b). Specimens were compared to materials in the University of Minnesota Insect Collection, which were available for all but *M. frugalis* females, and specimen photographs were reviewed by Jason Gibbs. Bees are deposited in the University of Minnesota Insect Collection; photographs are included in Fig. 1 and within the Minnesota Bee Atlas Species Guide (University of Minnesota Extension 2020).

After the emergence season, the *M. frugalis* and *M. inimica* nest tunnels were split open. Nests were photographed and measured using digital calipers and the Olympus cellSense Standard program. Composite photographs of the nests were created using the Olympus cellSense Standard, CombineZP, and Paint programs. A voucher nest for each species is housed in University of Minnesota insect collection. The *O. georgica* nest tunnel was not opened, because these bees were not identified until after block disposal. Nest descriptions for *O. georgica* can be found in the literature (*e.g.* Hartman et al. 1944, Krombein 1967, Hawkins 1975).

Table 1: Summaries of nesting records of Megachile (Sayapis) which inhabit the United States, encompassing the varying levels of information available.

Species	Location	Substrate	Materials and construction	Reference
M. fidelis	Sequoia Natl. Park, CA, USA	"small log"	1 nest.	Mitchell 1937
M. fidelis	Central Valley, CA, USA	pine trap nests	25 nests, 6.5–8.0 mm diameter.	Barthell et al. 1998
M. fidelis	San Joaquin Valley, CA, USA	Wooden trap nests	NA	Frankie et al. 1998
M. frugalis	Near Bingham Lake, MN, USA	pine/ Douglas fir wooden nesting block	1 nest, 7.94 mm diameter. Eight cells av. 10.1 mm long. Partitions made from leaf circles covered with masticated vegetation, which was also plastered on lower walls. Plug single layer of soil particles and masticated vegetation. Vestibule present.	This work
M. inimica inimica	San Antonio, TX, USA	"worm holes in mesquite trees or fenceposts."	Unknown number of nests. "Lined with circles cut from leaves of *Monisia pallida* Planch." (Probably *Celits pallida* Planch).	Mitchell 1937, H.B. Parks pers com.
M. inimica sayi	Sioux City, IA, USA	"mine in apple wood"	NA	Mitchell 1937, p 193
M. inimica inimica	Sand scrub in Florida, USA	Traps made from borings into wood	1 nest, 6.4 mm diameter. Cells 22–31 mm long. Partition before cells, cells unlined by leaf pieces, partitions "consisting of 1 or 2 circular leaf cuttings on the inner surface and 3-4 mm of agglutinated sand which also formed the base of the next cell." Vestibule 8 mm long, plug "17 mm thick of loosely arranged, more or less circular leaf cuttings."	Krombein 1967
M. inimica sayi	Desert floor, Arizona, USA	Traps made from borings into wood	2 nests, 6.4 mm diameter. Cells 17–25 mm long. Partition before cells. Partitions 1.5 or 2-3 mm thick, "had several leaf cuttings at the inner end then a layer of fine pebbles and leaf pulp". Vestibule 17 mm long. Plug 5 mm thick with leaf cuttings, pebbles and leaf pulp "which hardened into a firm plug."	Krombein 1967
M. inimica sayi	Ipswich, southern Wisconsin, USA	Sumac stem Traps	2 nests. Built against pith at tunnel bottom. "Not enclosed in pieces of leaf…but consisted only of the partitions formed of chewed leaf material."	Medler and Lussenhop 1968
M. inimica	Near Revere and Dover, MN, USA	pine/ Douglas fir wooden nesting block	5 nests, 6.35-9.53 mm diameter. Cells av. 12.8 mm long. Partitions made from one cut leaf piece, followed by a thin layer of soil particles, sometimes covered with chewed vegetation. Sometimes vegetation plastered on lower cell walls. Plug made of two layers of partitions with grass or wood pressed into it. No vestibule.	This work
M. newberryae	Arizona, USA	holes in *Prosopis*	Cutting leaves of *Celits*.	Butler 1965

Species	Location	Substrate	Materials and construction	Reference
M. pugnata	Wisconsin, USA	sumac stick trap-nests	20 nests, 6.25, 7.8 mm diameter, cells av. 15.27 mm long. "Cells were made with basal and apical partitions consisting of leaf discs, chewed leaf materials and soil." Vestibule present. Plug of layered partitions.	Medler 1964
M. pugnata	Captive rearing, Utah, USA	tunnels in elderberry, or glass tubes	Many nests. 8–9 mm diameter, some excavation. *Oenothera hookeri* for building material. Partitions made by masticating vegetation and smearing it on back and sides to make a rim. Leaf pieces attached to the rim, filling tunnel diameter. Another layer of masticated vegetation placed in a rim, smeared to the middle, and with soil particles pressed into it. Then "female laid on her back and groomed the posterior portion of the abdomen and again passed a droplet of liquid to the middle and fore-legs. This time the secretion was placed between the mandibles and chewed vigorously. The female then chewed and licked the outer surface of the partition." Almost all had vestibules.	Frohlich and Parker 1983
M. pugnata	Toronto, ON, Canada	Cardboard tube traps in PVC housing	45 nests. "Mud and chewed leaves to line its brood cells, and makes partitions between adjacent cells using circular pieces of leaves laid one over the other."	MacIvor 2016
M. policaris	Arizona and Florida, USA	Traps made from borings into wood	8 nests, 6.4 or 12.7 mm diameter. Single-larvae cells:13-30 mm long, communal brood cells: 17–78 mm long. "gummy leaf pulp" before cells, cells unlined by leaf material. Many large communal brood cells with multiple pollen balls or a long pollen ball. Partitions "2 layers of small compressed leaflets 2–9 mm long separated by thin septa of hardened, gummy leaf pulp. Occasionally several alternating layers . . . Closing plugs . . . were constructed of the same material in alternating layers." Vestibular cell frequently lacking. Leaf pieces from "*Prosopis* (mesquite), *Mimosa biuncifera* (cat claw acacia), *Eysenhardtia polystachya* (kidneywood)" and an unidentified shrub. Arizona bees used small whole leaflets vs circles.	Krombein 1967, W. Niles
M. zaptlana	Southern and coastal plains, Jamaica	"old beetle burrows in fence posts"	129 nests, cells av. 9.8 mm diameter. Cells av. 19.9 mm long. Base of the first cell lined with pieces of leaves and intercellular partitions constructed but longitudinal walls of cells unlined.	Raw 1984
M. zaptlana	Iguarassu, Pombos, PE, Brazil	Cardboard tubes in wooden traps, and wooden and clear plastic traps	157 nests, 6 mm diameter. Cells av. 6–9.3 mm long. Cells unlined by leaf pieces. Partitions between cells made of a rim of chewed leaves, followed by larger leaf pieces which were covered with chewed vegetation and sand. Most nests had 1 vestibule, some had up to 4. The final plug consisted of 2–5 juxtaposed partitions.	dos Santos et al. 2020

Table 2: Nests of new species records for Minnesota from 2018 season, with emergence dates of males (m) and females (f) listed in the timeline column.

Bee species	Minnesota County	Nest ID and tunnel diameter	Offspring	Emergence timeline
O. georgica	Winona Co.	502(F3) 4.76 mm (3/16 in.)	7	10-Mar-19: 2m 11-Mar-19: 4m 13-Mar-19: 1f
M. inimica	Cottonwood Co.	453(G2) 7.94 mm (5/16 in.)	4	1-May-19: 1m 7-May-19: 3f 9-May-19: 1f
M. inimica	Cottonwood Co.	453(H2) 7.94 mm (5/16 in.)	5	4-May-19: 2m 7-May-19: 3f
M. inimica	Olmstead Co.	467(D1) 9.53 mm (3/8 in.)	6	4-May-19: 6f
M. inimica	Olmstead Co.	467(E1) 9.53 mm (3/8 in.)	3	6-May-19: 2f 7-May-19: 1f
M. inimica	Olmstead Co.	467(E2) 6.35 mm (1/4 in.)	4	28-Apr-19: 1m 4-May-19: 1f Upon opening: 2f dead
M. frugalis	Cottonwood Co.	472(F2) 7.94 mm (5/16 in.)	8	15-Apr-19: 3m,1f 16-Apr-19: 4f

Results

Warming for emergence began on 4 March 2019 (Table 2). Six males and one female *O. georgica* emerged from a single nest between 10–13 March (Fig. 1). Three males and five female *M. frugalis* emerged from a single nest between 15–16 April 2019. Bees emerged from the five *M. inimica* nests between 28 April–7 May 2019. A total of *22 M. inimica* were collected, four males and 18 females, with an average of 4.4 bees/nest. In all cases above, males emerged before females within nests and there were no other organisms that emerged from these tunnels.

The *O. georgica* nest was in the 4.76 mm diameter tunnel F3 in block 502. The volunteer reported partial plugs of "mud/sand" on 2 June and 24 June 2018, and a full plug of the same material on 25 July 2018. Upon return to the University of Minnesota, we used the otoscope to record a complete outer nest plug of masticated vegetation, rather than mud/sand, which was a common misinterpretation among reporters. Despite frequent volunteer reports and helpful pictures of the five *M. inimica* nest blocks, nesting phenology information is sparse, possibly because these nests were plugged well inside tunnel entrances, making them difficult to see. Volunteer reports include grass material in 467(E1) on 7 July 2018, and a full plug of unknown material in 467(E2) on 28 September 2018. Upon return to the University of Minnesota, we recorded the following plug materials in the five tunnels that later produced *M. inimica:* three complete grass plugs, one complete plug of leaf/petal pieces, and one complete mud/sand plug. Variation in otoscope-recorded plug materials within a species can indicate incomplete nests, or that a species adds extra material to the final plug, or that another species has built a second nest in the tunnel, closer to the opening. Evidence from opening nest tunnels suggests the first two situations are likely for these nests as no evidence of other species' nests were seen. The *M. frugalis* nest was made in block 472(F2). The volunteer submitted six observations, with no activity in this tunnel. However, volunteer photographs show a full plug on 10 August 2018, which was absent on 22 July 2018, indicating the nest was completed between those dates. Upon return to University of Minnesota, we observed a full plug of masticated vegetation in the tunnel.

All five *M. inimica* nests were opened and a composite photograph of nest 453(H2) was created (Fig. 2). Four of the five nests were complete and measured on average 81.8 mm long, with final plugs recessed on average 26.2 mm from the tunnel entrance.

Three complete nests had five cells, one had six, and the incomplete nest had four cells. The average cell length was 12.8 mm (range: 8.3–17.6 mm). However, the cell lengths were longer in narrower diameter tunnels and shorter in wider diameter tunnels. The average cell length was 10.1 mm in the two 9.53 mm diameter tunnels, 14.0 mm long in the two 7.94 mm diameter tunnels and 15.7 mm long in the 6.35 mm diameter tunnel. In one nest, the innermost cell failed early, leaving a mass of pollen stores. In two other nests, there was a cell that did not produce an emerging adult, but these must have failed after cocoons were spun, as all cells contained evidence of cocoons. There was no evidence that the nests were parasitized, and no dead pupae or adults were found. Emerging bees can chew through dead offspring or adults, sometimes pushing debris out of the tunnel as they go and leaving little evidence behind. The average thickness of partitions between cells across all nests was 1.9 mm. The partitions were made from one whole leaf piece, followed by a thin layer of soil particles, in some cases with chewed vegetation on top. Cell walls were generally unlined by any leaf or soil material, although sometimes mud or masticated vegetation was spread part way up the sides of cells from the lower partition. The bees' cocoons were clearly evident, made of parchment-like material with yellowish orange frass distributed over the outside. No complete nest contained a vestibule. Despite the otoscope records of grass nest plugs, all final plugs consisted primarily of two consecutive partitions, of similar construction to cell partitions, with grass or wood fibers only pressed into the outermost surface of some. Plugs averaged 7.4 mm thick (range 6.6–8.3 mm).

The *M. frugalis* tunnel 472(F2) was opened and a composite photograph of the nest was created (Fig. 2). The nest had eight cells, corresponding to eight emerged adults. The nest occupied the full length of the 106.7 mm tunnel. Mud and possibly masticated vegetation were plastered on the innermost end of the nest, measuring 2.4 mm thick. The average nest cell length was 10.1 mm (range 9.6–10.7 mm) and partition thickness was 0.8 mm (range 0.3–1.1 mm). Each cell had a thin layer of masticated vegetation plastered on the inner 1/3–1/2 of the wall length, while the remaining wall area was covered with a shiny material over the bare wooden tunnel wall (Fig. 2). The bees' cocoons were clearly evident, made of parchment-like material with a small amount of brown frass, primarily on the outer ends. The upper partition of the last cell was made of two layers instead of one and measured 3.2 mm. All partitions were made of a single layer of leaf pieces, followed by a thin layer of masticated vegetation and sand. The nest contained a 13.1 mm long vestibule between the last cell and the final plug. The final plug was located at the tunnel entrance and composed of a single layer of soil particles mixed with masticated vegetation that was 2.3 mm thick.

Discussion

Our understanding of all three species' distributions is expanded somewhat northward by these new records for Minnesota. Among digitized bee records, the closest prior records for *O. georgica* are found in northern Indiana, Illinois, Kansas, and Missouri (GBIF.org 2020). It's also reported from nine counties in the Lower Peninsula of Michigan (Gibbs et al. 2017). *Megachile inimica* has been recorded in southern Wisconsin (Medler and Lussenhop 1968) and in Kalamazoo county in the Lower Peninsula of Michigan (Gibbs et al. 2017). The nearest digitized records are in Nebraska and Illinois (GBIF.org 2020). *Megachile frugalis* has also been recorded from eight counties in southern Michigan (Gibbs et al 2017) and there are also digitized records from Missouri and Kansas (GBIF.org 2020). Whether the northern records reported here are due to a change in the species' ranges or increased sampling effort is difficult to say from these data.

Our available nesting and emergence phenology point to mid or late summer nesting by *M. inimica* and *M. frugalis*. *Megachile frugalis* had clear nest plug data for late July to early August. The sparse nesting information for *M. inimica* nests came in July and September, somewhat corresponding to the flight period reported for southern Wisconsin of 4 July to 2 September (Medler and Lussenhop 1968). *Megachile inimica* also emerged at the very end of rearing, later than the rest of the bees. As we rear at fixed temperatures, and bee and wasp species emerge in a predictable order each year, the greater degree-days before emergence of *M. inimica* could point to a possible mechanism for the species primarily being found in areas with longer growing seasons. It also could point to a mechanism for a possible northward expansion of the species' distribution, as the freeze-free season in southern Minnesota has lengthened by 16 days from 1951–2012 (GLISA 2020).

Similarly, the full plug date for *O. georgica* reported by the volunteer (between 24 June and 25 July) would be late compared to other *Osmia* species seen in this project, which often complete nest building by early to mid-June. However, the partial plug noted by the volunteer in early June may actually represent the nest completion date, and the offspring emerged in the growth chamber in

the same timeframe as other small *Osmia*. Hawkins (1975) reports *O. georgica* completed nests between the end of May and the end of June in Tennessee.

With the addition of the *M. frugalis* nest in this work, seven of the eight (*Sayapis*) species in the US now have at least one record of a nesting substrate, or the material in which a nest is made (Table 1). Natural nests have been documented in wood substrates for *M. fidelis, M. inimica inimica* Cresson, *M. inimica sayi* Cresson, *M. newberryae* and *M. zaptlana* (Mitchell 1937, Butler 1965, Raw 1984). Others are only known from trap nests, which, while suggestive and in some cases well documented, does not necessarily fully encompass their nesting biology. For example, one predominantly ground nesting bee species, *Megachile wheeleri* Mitchell, has been caught in trap nests (Gordon 2000). O*smia lignaria* Say, which is managed using trap nests, can also nest in the ground (Rau 1937, Linsley and MacSwain 1941, Levin 1966). Other species may show flexibility in the use of nest substrate, such as *Megachile brevis* Say. This bee species can be found in trap nests, but also has been found in standing dead stems, in a termite hole in a garage door, among leaves — both alive and dead, in prostrate corn stalks, under cow chips and mats of prairie grass, among small rocks on the ground, and in holes actually in the ground (Michener 1953).

To date, internal nest architecture appears to be fairly conserved within the subgenus *Sayapis* in the United States. There is now information of varying detail for five of the eight species (Table 1). All available information indicates they construct nest cells that are unlined by leaf pieces, in contrast with most other *Megachile* which fully line the longitudinal walls of their nest cells with cut leaf pieces. Partitions between cells are also similar for these five (*Sayapis*) species, consisting of a layer of leaf pieces on the inner side covered with a mix of soil particles and masticated vegetation.

There are some differences between species. All United States (*Sayapis),* in contrast with many other *Megachile,* make use of soil particles in nest building to some degree. However, nest accounts indicate that the ratio of soil to masticated vegetation may differ between species in the subgenus. For example, we recorded final nest plugs of *M. inimica* covered with soil particles with grass or wood pressed into it, while the *M. frugalis* plug was primarily masticated vegetation. The *M. frugalis* nest also had masticated vegetation plastered on the lower walls of cells (Fig. 2), which is more wall lining than reported for *M. inimica* or *M. pugnata.* The *M. frugalis* nest contained a vestibule, similar to reports for *M. pugnata* and *M. inimica* (Medler 1964, Krombein 1967). In contrast, we did not see vestibules in our *M. inimica* nests. The most unusual nest structure in United States (*Sayapis*) is reported for *M. policaris.* This species can construct atypically large, multi-offspring cells (Krombein 1967, Michener 2007), unlike the more common single-offspring cells of *M. inimica, M. frugalis, M. pugnata and M. zaptlana (*Table 1; Medler 1964, Krombein 1967, Medler and Lussenhop 1968, Frohlich and Parker 1983, Raw 1984, MacIvor 2016, dos Santos et al. 2020). It is unknown to what degree nest architecture may naturally vary within a species or may differ between nests in trap nests compared to natural substrates.

It would be interesting to see how nest construction of other members of this subgenus compare to the five United States species that have been described. The nests of *M. fidelis* should be attainable from trap nests, and perhaps those of *M. newberryae* also. The final species, *M. mellitarsis*, has two intriguing synonyms (*M. terrestris_homonym* Cockerell 1908a and *M. geophila* Cockerell 1908b), which suggest affiliation for the ground, possibly indicating that it breaks from the other members of the subgenus and nests below-ground. However, Cockerell's (1908a) original description does not mention nesting, simply noting that the bee was flying close to the ground when caught. Future research could focus on nests of *M. mellitarsis,* as well as filling out nest architecture and natural substrate information for the other US (*Sayapis)* species. The results presented in this work add to foundational data on both bee distribution and nesting biology, addressing the lack of nesting information for bee species in the United States (Harmon-Threatt 2020).

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Multi-Year Biological Control of Black Vine Weevil, *Otiorhynchus sulcatus*, with Persistent Entomopathogenic Nematodes

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Abstract

The black vine weevil (BVW), *Otiorhynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae), has a worldwide distribution and is a serious pest of many agricultural crops with a host plant species range of 140 plants. Common economic losses occur in small fruits, including strawberries, ornamental and nursery plants, caused primarily by the root feeding larvae resulting in reduced vigor and plant death.

The susceptibility of BVW to entomopathogenic nematodes (EPNs) is well established with numerous authors publishing papers using a wide array of EPN species from commercial sources and very high application rates for use as a biopesticide. The concept of using native EPN strains that are climate adapted and retain the genetic traits of phased infectivity to persist across multiple years was successfully developed and tested on a related species, *Otiorhynchus ligustici* (L.), alfalfa snout beetle.

In this study, a single application of climate adapted persistent EPN strains resulted in a reduction of an economically damaging BVW population in strawberries to sub-economic levels. Subsequently, the BVW population remained undetectable for four years while the EPN populations remained moderately high.

Keywords: Black vine weevil, *Otiorhynchus sulcatus*, persistent entomopathogenic nematodes, biological control

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The black vine weevil (BVW), *Otiorhynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae), has a worldwide distribution (Willmott et al. 2002) with a host plant species range of 140 plants (Smith 1932), and is a serious pest of many agricultural crops. Common economic losses occur in small fruits, including strawberries, ornamental plantings and nursery plants (Fitters et al. 2001, van Tol et al. 2004). Economic damage is primarily caused by root feeding by the larvae (Smith 1932, Moorhouse et al. 1992), resulting in reduced vigor and plant death (Garth and Shanks 1978, LaMondia and Cowles 2005).

The susceptibility of BVW to entomopathogenic nematodes (EPN) is well established with numerous authors publishing papers using a wide array of EPN species from commercial sources. In these studies, EPN infective juveniles (IJ) were applied in water at very high rates and usually between 5 - 15 billion IJs per ha or 25,000 IJs per pot. If conditions are favorable and the IJs are alive, this biopesticide approach is effective at reducing BVW larval populations (e.g. Shanks and Agudelo-Silva 1990; Wilson et al. 1999; Fritters et al 2000, 2001; Georgis et al 2006; Lola-Luz and Downes 2007; Haukeland and Lola-Luz 2010).

The concept of using native EPN strains that are climate adapted and retain the genetic traits of phased infectivity to persist across multiple years was successfully developed and tested on a related species, *Otiorhynchus ligustici* (L.), alfalfa snout beetle (Shields et al 1999; Neumann and Shields 2006, 2008; Shields et al 2009; Shields and Testa 2017; Shields et al. 2018). These studies report the appropriate mix of EPN species from adapted strains, inoculated at a low rate to become established under field conditions, persisted for multiple growing season and suppress alfalfa snout beetle below economic levels. This research was the basis of an area wide biological control program against alfalfa snout beetle with over 8,000 ha inoculated to date (Shields and Testa 2017).

The focus of this study was to test the concept of biological control with persistent, climate adapted EPN strains against a related pest, BVW in the strawberry cropping system.

Materials and Methods

This study was conducted in a 4 ha strawberry planting of mixed ages with a high population of black vine weevil (BVW), *O. sulcatus* feeding on the roots and destroying the planting. The field was sandy loam and located east of Peru, NY, in Clinton Co. Preliminary larval sampling was conducted in June 2013, indicating a wide spread infestation across the entire 4 ha with an incidence of 50% of the plants being fed on by large larvae and many of the plants having multiple larvae feeding on their root system. The field was also sampled for the presence of naturally occurring entomopathogenic nematodes (EPNs). A replicated study was initiated in August 2013 with two treatments (Persistent EPNs and Untreated Check) with plots measuring 10 m × 10 m. Each treatment was replicated 4 times.

Nematode species and strains used. The EPN species/strains used in this study were *Steinernema feltiae* (Filipjev) 'NY 04' and *Heterorhabditis bacteriophora* Poinar 'Oswego'. *H. bacteriophora* 'Oswego' was initially isolated from soil samples collected in 1990 from Oswego County, NY and *S. feltiae* 'NY 04', was initially isolated from soil samples collected from Jefferson County, NY in 2004. To maintain the ability of these strains to persist under NY conditions, each species was re-isolated from the field every second year beginning in 2007, and used to reinitiate the laboratory culture (Shields and Testa 2015). The EPN strains used in this trial were re-isolated from NNY agricultural fields in 2013. Greater wax moth, *Galleria mellonella* (L.), larvae (Woodring and Kaya 1988) were used as hosts to maintain the nematode cultures. Between field isolations, culturing protocols have been modified to preserve the genes for persistence in the population during the two years of laboratory culturing (Shields 2015). A Galleria based non-white trap rearing system (Testa and Shields 2017) was used for the production of IJs for field application.

BVW larval sampling protocol. Individual plots were sampled for BVW larvae on 6/2013 (initial preliminary evaluation), 6/2014, 5/2015, 6/2015 (2×, early June and late June), 5/2016, 6/2016, 6/2017, 6/2018 and 6/2019. At each sampling date, 25 samples per plot were examined for the presence of BVW larvae. Each sample was taken centered over a strawberry plant with a Golf Cup Cutter (diameter 11 cm × 160 cm deep). The soil sample was removed, placed in a tray and examined for the presence of insect larvae. The number and instar of BVW larvae was recorded. Any insect cadavers infected with EPNs were also recorded. The percent of plants infested was calculated by dividing the number of infested plants found by the sample size (25). The number of larvae per plant was calculated by dividing the total number of larvae found by the number of infested plants per plot.

EPN sampling protocol. Individual plots were sampled for EPNs in 8/2013 (EPN application pre-sample), 10/2013 (40 days post inoculation), 5/2014, 9/2014, 5/2015, 9/2015, 5/2016, 9/2016, 5/2017, 9/2017, 5/2018 and 6/2019. At each sampling date, a total of 50 soil cores (2 cm × 20 cm) were collected from each plot and returned to the laboratory to be bioassayed for the presence of EPNs using Galleria larvae as indicator larvae. At the time of collection, the top 7 cm was placed in a 100 ml plastic cup with lid and the lower 13 cm was placed in a 240 ml cup with lid. Soil cores were divided in this manner to isolate *S. feltiae* in the upper layers from *H. bacteriophora* in the lower layers for the assay (Ferguson et al. 1995). Each container had a tight fitting lid. All soil samples were laboratory bio-assayed using *G. mellonella* larvae as indicator hosts (5 per 7 cm core, 10 per 13 cm core). Samples were incubated at room temperature (23°C), on shelves in the laboratory for 7 d. Dead *G. mellonella* were examined for nematode infection by observing the condition and color of the cadaver (Poinar 1984). Cadaver coloration between *S. feltiae* and *H. bacteriophora* is uniquely different and cannot be confused. Cadaver coloration suggesting possible *Steinernema carpocapsae* (Weiser), the most common wild EPN in NY were placed on moist plaster of Paris disks in Petri dishes (White 1927) ("White trapped"), and observed for IJ emergence. Isolated IJs were then used to infect *G. mellonella* larvae, dissecting out the adult males and verifying the EPN species with the shape of the male spicule head (Neumann 2007).

Initial EPN application. The initial application of EPNs was *S. feltiae* on 5 September 2013 and was scheduled to coincide with the presence of small instar BVW larvae in the planting. This species was originally selected because *S. feltiae* attack all size larvae including the smaller instars whereas *H. bacteriophora* prefers to attack the larger larvae after feeding damage has occurred (Neumann and Shields 2008). Approximately 3.6 million *S. feltiae* IJs were applied in 5 L of water (340 million IJs were applied in 500 L/ha) to each epn treated plot using an ATV mounted small plot sprayer equipped with fertilizer stream nozzles (TeeJet™ 0010, Springfield, IL). Application was made to the soil surface and was initiated late in the day (after 7 pm).

Subsequent EPN application. The spring 2014 BVW larval sampling indicated

Table 1. Percentages of strawberry plants infested with Black Vine Weevil, *Otiorhynchus sulcatus*, in the EPN treated plots over 6 years and the number of larvae per infested strawberry plant.

Date	% plants infested	Number of larvae per plant
6/2013	50 ± 0.7 a **	2.5 ± 0.37 a
6/2014	48 ± 0.07 a	2.0 ± 0.43 a
5/2015	48.7 ± 0.03 a	1.1 ± 0.09 b
6/2015 (early)	27.3 ± 0.03 a	1.0 ± 0.04 b
6/2015 (late)	17.3 ± 0.03 b	1.0 ± 0.03 b
5/2016	13.3 ± 0.03 b	1.0 ± 0.0 b
6/2016	7.0 ± 0.15 c	1.0 ± 0.0 b
6/2017	0 d	0 c
6/2018	0 d	0 c
6/2019	0 d	0 c

**Values within a column followed by the same letter are not significant different at the 0.01 level.

1) dead BVW larvae had been infected by *S. feltiae*, 2) *S. feltiae* had overwintered at a moderate level and 3) BVW population did not appear to be declining. The decision was made to add *H. bacteriophora* to the EPN population in the EPN treated plots. On 27 August 2014, approximately 4 million *H. bacteriophora* IJs were applied to each EPN treated plot using the previously described protocol (378 million IJs were applied in 500 L/ha).

Statistical Analysis. The study was designed as a randomized complete block design with four replications using two treatments (EPN & untreated). Presence of BVW was recorded as the number of plants (cores) infested with larvae and the number of larvae per plant (core). The number of plants infested was converted to percent infested and normalized with Arcsine transformation before analysis. The number of larvae per plant was averaged across the plot. Significant differences in infestation levels between sampling periods was tested using analysis of variance for a Random Complete Block Design (ANOVA) with post-hoc t-test applying Bonferroni correction (Systat Software Inc. 2009).

EPN population levels expressed in percent of soil samples with a positive bioassay for the presence of EPNs were normalized with Arcsine transformation before analysis. Significant differences in populations between years was tested using analysis of variance for a Random Complete Block Design (ANOVA) with post-hoc t-test applying Bonferroni correction (Systat Software Inc. 2009).

Results

BVW Sampling. Initial sampling in June 2013 for BVW larvae indicated 50.0 ± 0.7% of the plants were infested with 2.5 ± 0.37 larvae per plant in the plots to be treated with EPNs and 52.0 ± 0.3% of the plants infested with 2.5 ± 0.51 larvae per plant in the untreated plots. After the application of the EPNs, the percent of infested plants declined over time to undetectable (2013–2019) and the population of EPNs increased over the 6 year duration of the study (15% to 45% of the samples positive for EPN IJ).

Sampling in June 2014 and the first sampling in May 2015 indicated that the percentage of infested plants remained statistically identical (2014 = 48.0 ± 0.07%, 2015 = 48.7 ± 0.03%). The percent of infested plants decreased significantly during the second sampling in early June 2015 (27.3 ± 0.03% plants infested) ($F = 2.13$; df = 8; $P = 0.01$) and the third sampling in late June (17.3 ± 0.03% plants infested) ($F = 1.98$; df = 8; $P = 0.01$). A significant level of decreased infested plants continued in May 2016 (13.3 ± 0.1%, $F = 2.37$, df = 8, $P = 0.01$) and June 2016 (7.0 ± 0.15%, $F = 2.27$, df = 8, $P = 0.01$). Sampling for BVW in June 2017, 2018, 2019 found no plants infested with BVW larvae with levels significantly lower than the final sampling in 2015. ($F = 2.57$; df = 32; $P = 0.01$) (Table 1).

The mean number of larvae per infested plant decreased from 2 ± 0.43 (range 0 - 6) in the spring 2014 to 1.1 ± 0.09 in May 2015 and 1.0 ± 0.01 in May 2016, a statistically significant reduction ($F = 2.31$; df = 24; $P = 0.01$). All larval counts were statistically different from each other ($F = 2.01$; df = 11; $P = 0.01$) (Table 1).

In the untreated check plots, the BVW larvae initially infested 52 ± 0.3% of the plants in 2013. These levels were not statistically different from the initial levels in the plots treated with EPNs (50 ± 0.7). During the 2014, the percentage of infested plants increased to 86 ± 0.4% of the plants. A significant increase over the initial levels in 2013 ($F = 2.03$; df = 3; $P = 0.01$). The ini-

Table 2. Percentages of soil samples bioassayed positive for entomopathogenic nematode species *Steinernema feltiae* and *Heterorhabditis bacteriophora*.

Date	*S. feltiae* $\bar{x}$% ± *SE*	*H. bacteriophora* $\bar{x}$% ± *SE*	Combined $\bar{x}$% ± *SE*	Days after application
10/2013	12.8 ± 3.0 a**	0 a	12.8 ± 3.0 a	35
6/2014	14.7 ± 2.5 a	0 a	14.7 ± 2.5 a	270
8/2014	15.0 ± 4.0 a	0 a	15.0 ± 3.0 a	330
5/2015	11.5 ± 2.0 a	3.9 ± 2.2 b	15.5 ± 1.9 a	600
9/2015	15.9 ± 1.3 a	9.0 ± 1.1 c	24.9 ± 2.1 b	720
5/2016	27.5 ± 4.2 b	10.0 ± 2.7 c	37.5 ± 3.4 c	960
9/2016	16.6 ± 6.5 a	13.0 ± 6.5 c	29.6 ± 6.5 bc	1,080
5/2017	15.8 ± 3.3 a	8.3 ± 3.2 c	24.1 ± 3.1 b	1,320
9/2017	24.8 ± 1.0 b	2.0 ± 2.0 b	26.8 ± 1.5 b	1,440
5/2018	24.0 ± 4.0 b	2.0 ± 1.0 b	25.8 ± 4.0 b	1,680
6/2019	45.0 ± 2.0 c	0 a	45.0 ± 2.0 d	2,075

**Values within a column followed by the same letter are not significant different at the 0.01 level.

tial mean number of larvae per plant in the untreated check plots (2.5 ± 0.51 larvae) was not significantly different than the initial larval levels in the plots treated with EPNs (2.0 ± 0.43 larvae).

The mean number of larvae per plant in the untreated plots significantly increased from 2.5 ± 0.51% of the plants (range 0–6) in May 2014 to 4.2 ± 0.23 larvae per plant in May of 2015 ($F = 2.13$; df = 3; $P = 0.01$). By July 2015, the plant stands in the untreated check plots were completely destroyed.

EPN sampling. Results from the EPN pre-treatment bioassay of soil cores indicated no native populations of *S. feltiae*. The presence of a native *H. bacteriophora* was discovered in less than 2% of the soil samples. Forty days after *S. feltiae* application (10/2013), soil core bioassay indicated 12.8 ± 3.0% of the cores with *S. feltiae* and 1.86 ± 1.0% of the cores with *H. bacteriophora* with a combined EPN positive cores of 14.7 ± 3%. In early June 2014, EPN sampling indicated 14.7 ± 2.48% *S. feltiae* and 3.6 ± 1.5% *H. bacteriophora* with a combined total of 18.2 ± 3% EPN positive soil cores. In August 2014, before the supplemental application of *H. bacteriophora*, the EPN levels were, 15 ± 4.0% *S. feltiae* , 0% *H. bacteriophora* and 15 ± 3.0% combined. In May 2015, EPN population levels were, 11.5 ± 2.0% *S. feltiae*, 3.9 ± 2.3% *H. bacteriophora* and 15.5 ± 1.9% combined. In September 2015, EPN population levels were 15.9 ± 1.3% *S. feltiae*, 9.0 ± 1.1% *H. bacteriophora* and 24.9 ± 2.1% EPN combined total. Spring sampling in May 2016 indicated, 27.5 ± 4.2% *S. feltiae*, 10 ± 2.7% *H. bacteriophora* and a combined EPN total of 37.5 ± 3.4%. Fall sampling in September 2016 indicated 16.6 ± 6.5% *S. feltiae*, 13.0 ± 6.5% *H. bacteriophora* and a combined total of 29.6 ± 6.5%. Spring sampling in May 2017 indicated, 15.8 ± 3.3% *S. feltiae*, 8.3 ± 3.2% *H. bacteriophora* and an EPN combined total of 24.1 ± 3.1%. Fall sampling in September 2017 indicated 24.8 ± 1.0% *S. feltiae*, 2.0 ± 2.0% *H. bacteriophora* with a EPN combined total of 26.8 ± 1.5%. May 2018 indicated 24.0 ± 4.0% *S. feltiae*, 2.0 ± 1.0 *H. bacteriophora* with a combined total of 25.8 ± 4.0%. Spring of 2019 indicated 45.0 ± 2.0% *S. feltiae* and 0% *H. bacteriophora* (Table 2).

The increase in total EPN populations (both species combined) was significant in Sept. 2015 and then again in June 2019. EPN population levels were not significantly different between Oct 2013 and May 2015 (16% of the soil samples positive for EPN). In Sept 2015, the EPN population increased significantly from the previous level and remained at the significantly higher level until May 2018 (32% of the soil samples positive for EPN). In June 2019, the EPN population increased to a significantly higher level (45% of the soil cores positive for EPN).

BVW populations decreased over time with a corresponding increase of EPN levels. All of the dead larvae observed during soil sampling for larvae displayed symptoms of EPN infection. Larvae were not observed with any pathogenic fungi infection. Regular sampling of the untreated check plots for EPNs indicated no movement of EPNs into the untreated check areas during the duration of the experiments.

Discussion

During the duration of the study, no insecticides were used to suppress the BVW adult populations. The focus of the study was to see if persistent EPNs alone could reduce the economically damaging levels of BVW to a sub-economic level and maintain the BVW population levels below economic damaging levels for multiple growing seasons. This

study suggests that EPNs can be utilized in a classical biocontrol strategy where the soil is inoculated with a relative low rate of EPNs which are climate adapted and retain the genetic ability to persist in the soil environment for multiple years including across months of frozen soil each winter. In addition, the EPN species mix was selected to overlap with the soil profile of the insect host to provide maximum opportunity for the EPNs to attack and recycle in the target host. The inoculation rate for both species combined was only 29% of the typical EPN application rate when EPNs are used as a biopesticide (720 million/ha vs. 2.5 billion/ha).

Steinernema feltiae 'NY04' was initially selected because it prefers small larvae which are attacked before significant root feeding occurs (Neumann and Shields 2008), its lower temperature threshold of host infection is 6°C (Neumann 2003) and it preferred soil profile niche was the top 20 cm of the soil. These characteristics were considered a better match to the temperature activity thresholds of black vine weevil larvae in the spring feeding on strawberry roots. In addition, *S. feltiae* 'NY04' has demonstrated its ability to persist for multiple years at a moderate population level (20–30% of the soil cores) in the NY agricultural system (Shields et al. 2018). The lack of host reduction 10 months after *S. feltiae* inoculation suggested that *S. feltiae* may not be able to reduce an economically damaging population of black vine weevil to sub-economic levels on a timely basis without help. At this point, *H. bacteriophora* 'Oswego' was applied to assist *S. feltiae* with the biocontrol of black vine weevil. *H. bacteriophora* 'Oswego' also was adapted to NY agricultural conditions, retained its genetics to persist for multiple season under NY conditions, has the lower temperature of infectivity at 8°C (Neumann 2003), soil profile niche of the top 30 cm of the soil and prefers sandy soils. The two less desirable characteristic were the higher temperature threshold of activity and the preference to attack larger larvae, allowing root feeding damage by the insect before being attacked by *H. bacteriophora.*

The trends of EPN populations was interesting. There appeared to be a significant lag period of 22 months before the EPNs were able to reduce the black vine weevil larval populations to a sub-economic level. In addition, it appeared to require a similar period before the EPN populations began to increase in the research plots. In 2016, peak EPN populations coincided with the significant decrease in black vine weevil populations. Starting in 2017, black vine weevil larvae were not detected in the EPN treated plots for the remainder of the study (3 years). With the absence of black vine weevil hosts, the population levels of *H. bacteriophora* declined to undetectable in 2019 while the population levels of *S. feltiae* increased. Interestingly, in 2019, the population of *S. feltiae* peaked at its highest level in 2019, suggesting an invasion of susceptible hosts even though black vine weevil larvae were not detected in a 2019 sampling. While strawberry yields were not recorded, the grower reported increased yields each year that the levels of BVW were reduced. This impact is also supported with the total destruction of the untreated check plots within 24 months. Subsequently, the grower has inoculated his entire strawberry and blueberry acreage against BVW.

Over 2,000 days after inoculation, a significant population of *S. feltiae* (45% of the soil cores) continues to be present in the treated plot areas ready to infect susceptible insect hosts which invade the area. Shields et al. (2018) indicates that this strain of *S. feltiae* will persist in the soil for multiple growing season going forward in time. A continuing questions is whether this persistent population of *S. feltiae* will prevent the buildup of an economic population of black vine weevils in future years.

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Occurrence of Ticks (Acari: Ixodidae) on Birds in Northwestern Lower Michigan, 2011–2019

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Abstract

Monitoring tick infestation of wildlife provides baseline tick occurrence data that may have human or animal health implications. We collected 312 ticks of four species from 5,122 birds of 93 species while monitoring bird migration during 15 fall and spring seasons between 2011 and 2019 in the northern Lower Peninsula of Michigan. Twenty-seven of 93 bird species hosted ticks with an overall prevalence (= at least one tick) of 3.6% (185/5,122). Median burden was one tick/per infested bird with a range of 1–16 ticks per infested bird. Tick species collected were primarily *Haemaphysalis leporispalustris* (Packard) and *Ixodes scapularis* Say, with smaller numbers of *Ixodes dentatus* Marx and a single *Ixodes brunneus* Koch. The prevalence of avian infestations by *I. scapularis* increased over the eight-year study period (*P = 0.046*) to a high of over 4.6% infestation by *I. scapularis* in 2019. Based on the migratory status of birds, our data suggest that birds transported ticks to our site from northern or southern areas. Additionally, based on bird recapture data during stop-over periods at our site, we detected new tick infestations in 27 of 437 birds that had ticks removed on initial capture. These reinfestations potentially reflect bird's local acquisition of ticks, such as *I. scapularis*. This indicates that *I. scapularis* is becoming established in the region, which appears to be on the leading edge of this tick's expanding range in the Lower Peninsula of Michigan. Birds may be contributing to the establishment by contributing and possibly introducing and maintaining the ticks. Birds may be transporting ticks and seeding them elsewhere.

Keywords: ticks, phenology, pathogen, vector, zoonotic, birds

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Surveys that focus on associations among tick vectors and avian hosts provide useful data complementing the studies focused on tick-borne pathogens and disease risk (Ogden et al. 2008, Hamer et al. 2011, Loss et al. 2016, Clow et al. 2017, Walter et al. 2017, CDC 2018, Sonenshine 2018). In these surveys, infestation prevalence and the number of ticks on birds (hereafter burden) have been related to factors such as host status (migrant, breeding resident, year-round resident), body size, foraging height or location, phenology of tick life stages, and vegetation structure (Ogden et al. 2008, Loss et al. 2016, Parker et al. 2017). We collected ticks from migrating birds in the NW Lower Peninsula of Michigan to provide an overview of all ticks encountered relative to characteristics of bird species that may influence tick prevalence and burden. We then examined changes in annual prevalence over the 9-year study for two tick species most common in the region. Human health concerns vary depending on tick species and pathogens (Nelder et al. 2016, Loss et al. 2016, CDC 2018, Sonenshine 2018, Scott et al. 2020), although most human-biting ticks and tick-borne pathogens are maintained in wildlife populations. Thus, ecological studies focused on documenting tick-host associations over time, especially in regions of tick range expansions, provide crucial information to complement epidemiological and disease-focused studies.

Materials and Methods

Study Site. From 2011–2019, we used 12 × 2.6 m mist nets, with a mixture of 32 mm and 36 mm mesh sizes, to capture birds.

Figure 1. Tick infested Indigo Bunting, *Passerina cyanea* (L.) from the Chippewa Run Natural Area in the northern Lower Peninsula of Michigan. photo by Alice Van Zoeren.

Ten nets were opened with reduction in number of nets in times of heavy flights. Nets were placed at the Chippewa Run Natural Area (44.81°N, 86.05°W), near Empire, Leelanau County, Michigan. Shrubby vegetation 0.5–2.5 m in height consists of Honeysuckle (*Lonicera tatarica* L.), willows (*Salix* sp.), and Red Osier Dogwood (*Cornus amomum* Mill.). The shrubs are interspersed with taller Paper Birch (*Betula papyrifera* Marsh.) and Pin Cherry (*Prunus serotina* Ehrh.). This shrub-woodland was bordered by a variety of grasses and forbs on the upland side and a cattail (*Typha latifolia* L.) marsh with flowing water on the lowland side. Mist nets were opened seven days per week at sunrise for 3–4 hours, weather permitting, for a total of 8,463.05 net hours for seven spring seasons and eight fall seasons. We netted, in most seasons, from 1 May through 31 May and from 15 August through 30 September. No data from 2012 were available for analysis because of laboratory mis-handling.

Bird Processing. Captured birds were aged, sexed, weighed, and banded with U.S. Geological Service bands. Each band is uniquely numbered to allow tracking of individuals. After search and removal of ticks, the birds were released. Following banding protocol, birds were aged as after hatch year (AHY) in the spring and hatch year (HY) or AHY in the fall using accepted criteria (Pyle 1997). Birds were released after searching for and removing any ticks. Federal and State of Michigan bird banding permits to Scharf allowed the work described here.

Bird species status was designated as migrant, breeding/migrant, or year-round non-migratory resident (see Chartier et al. 2011) because noting that status could be important in infestation by ticks (see Loss et al. 2016). Bird foraging height followed categories of Parker et al. (2017): designating canopy, or below the canopy, or ground foraging. Bird names in the Supplement follow the International Ornithological Congress (IOC) list which and includes authors (Gill et al. 2020).

Tick Collection. Each bird was closely examined for the presence of attached ticks, especially around the head and neck with particular attention to the ear region and eyelids (Fig. 1). A head-mounted magnifying loupe facilitated inspection and removal of ticks. Ticks were removed intact with

Table 1. Distribution of 312 ticks by life stage and season. Ticks were removed from birds captured during fall and spring seasons of 2011–2019 in the northeastern Lower Peninsula of Michigan.

Species and season		Adult	Larvae	Nymph	undetermined	Total
Haemaphysalis leporispalustris	Total		122	29		151
	fall		106	18		124
	spring		16	11		27
Ixodes brunneus	Total	1				1
	spring	1				1
Ixodes dentatus	Total		11	4		15
	fall		5	1		6
	spring		6	3		9
Ixodes scapularis	Total		62	80		142
	fall		57	8		65
	spring		5	72		77
Ixodes species	Total		1	1	1	3
	spring		1	1	1	3
Total		1	196	114	1	312

fine, straight forceps taking care to remove the entire tick for later identification.

Typically, during migration, birds stop along the route to replenish fat and energy stores (Kaiser 1999). Time between initial examination and recapture within a season provided a minimal estimate of stopover length of bird migrants. During stopover periods, banding, removing ticks when found, then inspecting recaptured birds for ticks, provided an indication that ticks were locally acquired.

All ticks removed from birds were preserved in labeled vials containing 70% ethanol. The ticks were identified by S. A. Hamer and L. Auckland at Texas A&M University to species and stage in 2013 - 2019. Dr. Jean Tsao of Michigan State University identified ticks from 2011. Tick specimens are deposited in the Texas A&M University tick collection.

Statistical Analysis. Data were analyzed using Minitab 19 (2020). Infestation prevalence was compared using Wilcoxon-Mann-Whitney two-sample signed rank tests (Zar 1999) tests with two-tailed probabilities, including tests of differences in infestation by season and bird age (Parker et al. 2017) and body size of bird (Marsot et al. 2012, Brinkerhoff et al. 2018).

Results

In total, 5,122 birds (includes recaptures) of 93 species were examined during fall and spring seasons between fall 2011 and fall 2019, excluding 2012 (Supplement). Ticks were collected from 29% (27/93) of bird species captured (Supplement). Of these tick bearing birds, only six were year-round non-migratory species and only one in this group, a Northern Cardinal (*Cardinalis cardinalis* [Linnaeus]), hosted a tick (Supplement). Excluding, 680 year-round residents and within season recaptures, the mean initial capture date in the spring was 17 May (N = 2,429 birds, SD = 8.0 days) and the mean capture date in the fall was 7 September (N = 2,013 birds, SD = 11.6 days). Based on these initial capture dates and status, 87% (4,442/5,122) of birds were migrants.

We collected 312 ticks from 2,382 and 2,740 birds from spring and fall, respectively. The overall infestation prevalence was 3.6% (185 of 5,122 birds hosted at least one tick) (Table 1). Tick burden ranged from 1-16 ticks, with a median of one tick/per infested bird (Fig. 2). For comparison to other studies (e.g., Loss et al. 2016), the mean for our study was 1.6 ticks/infested bird.

Bird species were categorized by foraging category of ground-understory or canopy (Loss et al. 2016, Parker et al. 2017) for species with more than 10 individuals sampled (see Loss et al. 2016, Brinkerhoff et al. 2018). Only 1 of 23 (4%) of canopy foraging species was infested (an American Redstart, *Setophaga ruticilla* (Linnaeus)), which was significantly fewer than 74% (23/31) ground-understory birds that hosted ticks (*Fisher's Exact Test* = 0.0000002).

To assess variation in the prevalence of infestation by season and age, we used the 25 bird species that were captured in both

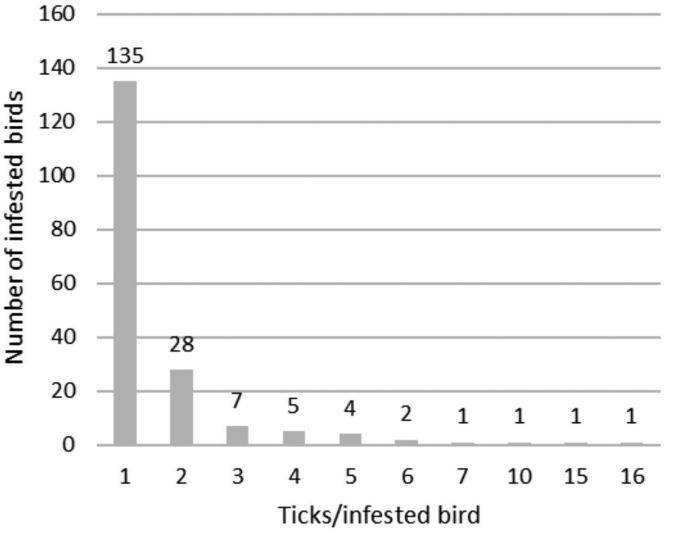

Figure 2. The distribution of 312 ticks on 185 bird hosts.

seasons and found no significant difference related to season (*Mann-Whitney-Wilcoxon* = 684; df = 25,25; $P = 0.369$) (Table 2) or age (*Mann-Whitney-Wilcoxon* = 563.5; df = 25,25; $P = 0.138$) (Table 2). To assess variation in the prevalence of infestation by bird weight, we used bird species that were infested and had 10 or more individuals sampled, for which our data showed no relationship ($R^2 = -0.078$, $P = 0.692$) (Fig. 3)

We collected four species of ticks: *Haemaphysalis leporispalustris* (Packard), *Ixodes brunneus* Koch, *Ixodes dentatus* Marx, and *Ixodes scapularis* Say. Tick species, percent of total ticks (n = 312), and percent of infested birds with the tick species in order were: *H. leporispalustris*, 48.4% (151/312) of ticks on 34.1% of infested birds, *I. scapularis,* 45.2% (142/312) of the ticks on 58.4% of infested birds; and *I. dentatus,* 4.8% (10/312) of ticks found on 5.4% of infested birds. We collected a single *I. brunneus* (Keith et al. 2015), and three *Ixodes* sp. ticks could not be identified to species (Table 1).

Two tick species, *I. scapularis* and *H. leporispalustris*, were numerous enough to provide assessments of phenology for larvae and nymphs. We found the overall number of *I. scapularis* were similar in fall and spring, but there were significantly more *I. scapularis* nymphs in the spring (*Chi-square* = 102.595; df = 1; $P < .00001$) and more larvae in the fall (Fig. 4A). In contrast, fewer *H. leporispalustris* were found in the spring than fall. In this species, larvae were more common than nymphs in both seasons, but similar to *I. scapularis*, there were significantly more larvae in the fall (Fig. 4B) (*Chi-square* = 9.827; df=1; $P = .00172$).

The annual prevalence of *I. scapularis* infestation increased from 1.5% to 4.85% at a rate given by the slope of the regression of 0.55% (Fig. 5) ($R^2 = 0.58$, $P = 0.046$). This regression was based on 2013 - 2019 when sampling was done in both fall and spring. In

Table 2. Summary values for percent prevalence of infestation for 25 (=N) bird species birds examined during fall and spring. Categories include All-Fall = AHY+HY, only AHY birds are encountered in spring. Means and SEs are provided for comparison to other studies. Q1 and Q3 refers to the first and third quartile about the median. Superscripts refer to comparisons (see text) that were not significantly different (p>.05).

Variable	N	Minimum	Q1	Median	Q3	Maximum	Mean	SE Mean
All-Fall[1]	25	0	1	5	13	100	13	4
AHY-Fall[2]	25	0	0	0	7	31	5	2
HY-Fall[2]	25	0	0	6	13	100	13	5
AHY-Spring[1]	25	0	0	5	11	20	6	1
Overall	25	0	2	5	10	20	6	1

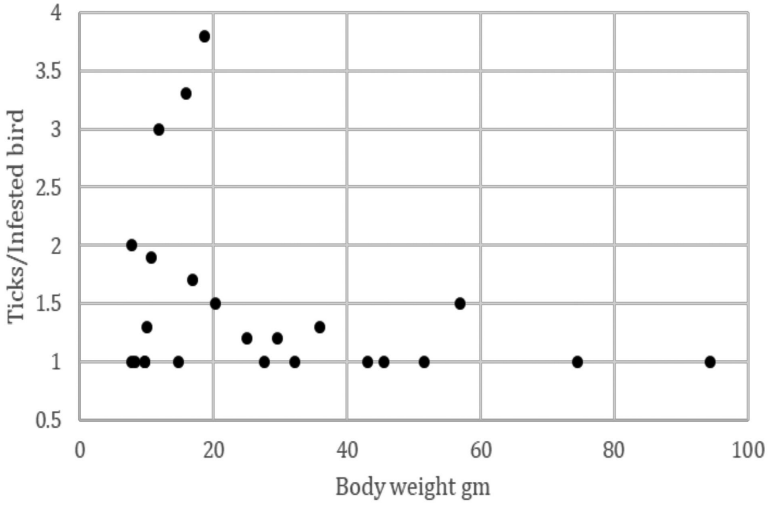

Figure 3. Average body weight relative to tick burden for bird species that had 10 or more individuals examined. See Supplement for species and sample sizes.

contrast, the annual *H. leporispalustris* infestation prevalence was relative unchanged across this period with approximately 1.2% infestation prevalence ($R^2 = 0.038$, $P = 0.673$) (Fig. 5). Percent data used in regressions did not deviate significantly from normality (*I. scapularis, Anderson-Darling* = 0.402, N = 7, $P = 0.256$; *H. leporispalustris, Anderson-Darling* = 0.250, N = 7, $P = 0.618$).

Of 27 bird species with ticks, 23 species hosted *I. scapularis* and 19 species hosted *H. leporispalustris* separately. Individual bird infestation by more than one species of tick at the same time occurred rarely, with five birds hosting both *I. scapularis* and *H. leporispalustris* and one bird hosting both *I. dentatus* and *I. scapularis*.

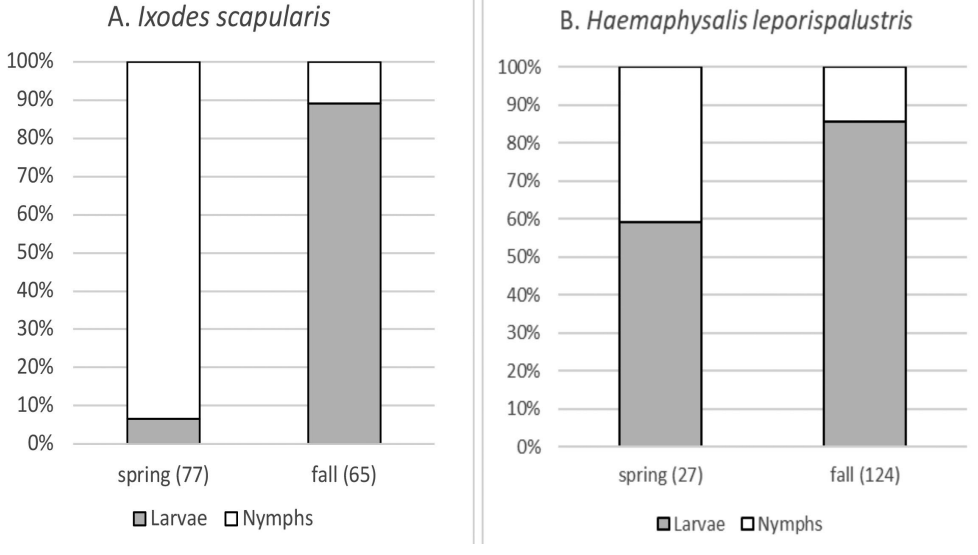

Figure 4. Percent of each life stage in relation to the total number of ticks removed from birds in spring versus fall, 2011–2019. Sample size of birds examined was 2,382 in the spring and 2,740 in the fall.

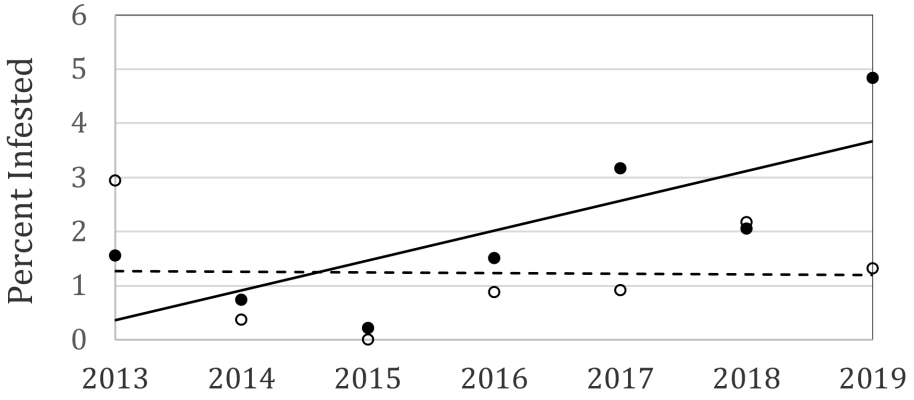

Figure 5. Prevalence of infestation on birds for *I. scapularis* (solid marker & solid trend line) and *H. leporispalustris* (open marker and dashed trend line) using years with fall and spring netting. *I. scapularis* increased, while *H. leporispalustris* was unchanged. Regression *I. scapularis* y = 0.5513x – 1109.4, *H. leporispalustris* y = –0.0121x + 25.704. Year-birds examined: 2013-577, 2014-538, 2015-461, 2016-793, 2017-979, 2018-826, 2019-681.

Origin of Ticks. Birds were categorized as migrants or migrants that breed locally with the exception of six non-migratory species that are year-round residents at the field site (Supplement). The analysis of within season recaptures of 437 birds allowed a conservative estimate of stopover length (Kaiser 1999) and local infestation. The median stopover length was four days (quartiles about median = two and eight days). Of these same-season recaptures, 6.2% (27/437) hosted ticks when recaptured (Table 3), including *I. scapularis* and *H. leporispalustris*, indicating that both these tick species could have been be acquired locally (Table 3).

The criteria used to designate an established tick population is either at least six or more individuals or two of more life stages identified in a single collection period (Dennis et al. 1998), with collection period further defined as a single year (Eisen et al. 2016). A simple tally of ticks removed from birds (Table 4) has limited utility in designating the establishment status of ticks at a field site, because ticks may be imported from other areas on migrants. However, analysis restricted to the new tick infestations on recaptured birds, during a time when avian movements outside of the study area are not expected, is useful in establishing the local origin of ticks (Table 5). Based on this restricted analysis, both *H. leporispalustris* and *I. scapularis* met criteria of established tick populations for three and four years within the eight years of study, respectively.

Discussion

We found 3.6% of birds captured during spring and fall migrations in 2011–2019 harbored ticks of four different species. *H. leporispalustris* and *I. scapularis* were most common. A systematic review of bird-tick publications from North America showed an overall infestation prevalence of 5.1% (Loss et al. 2016). Similar studies from the midwestern Unites States report overall infestation prevalence of 12.5% (Wisconsin, Nicholls and Callister 1996), 1.6% (Illinois, Hamer et al. 2012), 10.6% (Michigan, Hamer

Table 3. Tick species and stage found on 27 of 437 birds recaptured during stopover periods. No ticks were found on 410 recaptured birds. Birds are assumed to have remained in the study area during the stopover periods.

	Larvae		Nymphs		Total	
Tick species	**Ticks found**	**Birds examined**	**Ticks found**	**Birds examined**	**Ticks found**	**Birds examined**
Haemaphysalis leporispalustris	18	6	8	5	26	11
Ixodes dentatus	1	1			1	1
Ixodes scapularis	14	9	8	6	22	15
Totals	33	16	16	8	49	27

Table 4. Ticks found on all birds by year and season.

	Fall		Spring	
Year	Larvae	Nymph	Larvae	Nymph
	Haemaphysalis leporispalustris			
2011	41	5		
2013	15	5	7	8
2014	3		1	
2016	6	3		
2017	14	1	1	2
2018	20	3		4
2019	7	1	3	1
	Ixodes scapularis			
2011	5			
2013	4	4		8
2014				4
2015	1			
2016	5		2	6
2017	12	2		19
2018	4	2		18
2019	26		3	17

Table 5. Tick reinfestation of birds during migratory stopover. used to evaluate criteria for demonstrating the establishment of tick populations. Using Eisen et al.'s criteria, both tick species would be categorized as established.

	Fall		Spring	
Year	Larvae	Nymphs	Larvae	Nymphs
	Haemaphysalis leporispalustris			
2011	5	4		
2013	4		3	1
2016		1		
2018	4	2		1
2019	1			
	Ixodes scapularis			
2011	1			
2013	1	2		1
2016	2		1	2
2017	3			2
2018	1			1
2019	5			

et al. 2011), and 13.2% (Illinois, Parker et al. 2017). Tick burdens on birds varied from a median single tick in this study to two ticks/infested bird in Northcentral Wisconsin 1989-1992 (Nicholls and Callister 1996).

Haemaphysalis leporispalustris was the most abundant tick in our study, and accounted for 48% of the ticks. An overview of North American bird-tick data found that *H. leporispalustris* accounted for 30.1% of ticks on birds using data from across 11 studies (Loss et al. 2016). In netting studies like ours, there was wide variation in how common *H. leporispalustris* was on sampled birds. For example, this tick species accounted for 66.2% of bird ticks in Minnesota (Brinkerhoff et al. 2018), 45% of bird ticks in Illinois (Parker et al. 2017), 98% of bird ticks in Wisconsin (Nicholls and Callister 1996), 8.3% in Illinois (Hamer et al. 2012), and 13.4% in Michigan (Hamer et al. 2011). The widespread occurrence of this tick, which can harbor pathogens, may be of limited human health consequence since this species feeds almost exclusively on birds and rabbits and they rarely bite humans (Lane et al. 1991, Nicholls and Callister 1996, Hamer et al. 2011).

Ixodes scapularis comprised 45% of bird ticks in our study. This tick was the most commonly reported bird tick in systematic analysis of bird tick data from North America, accounting for 62% of ticks on birds (Loss et al, 2016). In contrast to our findings, at a study site in Michigan 260 km south of our site, *I. scapularis* accounted for less than 1% of ticks while *I. dentatus* accounted for 86.6% of ticks in 2004–2009 (Hamer et al. 2011). This difference could reflect geographic and habitat differences (Hamer et al. 2010, Parker et al. 2017), as *I. dentatus* was associated with inland areas while *I. scapularis* was found in coastal areas. However, the difference may also be explained in that *I. scapularis* has been undergoing a range expansion in Michigan with documented expansion in the Lower Peninsula, such that tick community compositions have likely changed over the last decade. For example, surveillance at a field site along the east shore of Lake Michigan only 12 km SW of our field site failed to detect *I. scapularis* for several years until a small number of *I. scapularis* were first detected on small mammals in 2008, representing a northward expansion into the region (Hamer et al. 2010). Our study indicates continued expansion of *I. scapularis,* which now accounts of half of the ticks encountered on birds.

Ticks may be carried into the area by migrating birds or of local origin. Using Eisen et al.'s (2016) criteria and specifically restricting our data analysis to ticks that were acquired on site (rather than those that arrive on migrating birds), we showed that *H. leporispalustris* met criteria of an established population in three of eight years at our study site. Similarly, *I. scapularis* met the criteria in four years of our study. Given that tick collection from birds is influenced by the search effort/sample size, it is likely that increased efforts in future years will

continue to show establishment of these species at the site.

We found that foraging height was a significant factor related to tick prevalence or on bird hosts, which was expected (Loss et al. 2016, Parker et al. 2017, Brinkerhoff et al. 2018). A second expected relationship of tick burden to body mass was not confirmed by our data. Again, a lack of a relationship may reflect a different bird species profile of our sample in that there was not a dispersion of bird weights of infested birds (Supplement) similar to other studies (Marsot et al. 2012, Brinkerhoff et al. 2018).

Ground-foraging bird species, especially non-migratory ground foragers, were disproportionately likely to have high prevalence and burden of ticks (Mitra et al. 2010, Loss et al. 2016). However, most of the bird species we sampled were migrants with only 6.5% (6/93) of bird species non-migratory. Only one of these, Northern Cardinal, was a ground foraging species (Supplement). Accordingly, given the focus on migrants and a lack of ground foraging resident at northern latitudes, we were unlikely to find that ground foraging resident birds as being disproportionately infested with ticks. In regions where ground foraging resident species are rare, migratory birds maintain of the tick populations and concomitant the enzootic cycles.

Acknowledgments

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Supplement. Prevealance and abundance of ticks on birds species examined in fall 2011 and spring and fall 2013-2019.
Status YR=year-round non migratory resident, MB=migrant or breeding, M=migrant
Where typically found, categories: G-U = ground or understory, C=canopy
Species names and authors follow International Congress of Ornithology. Gill, F., D. Donsker and P. Rasmussen, P (Eds). 2020. IOC World Bird List (v 10.1).

Species	Status	Birds examined	Birds with a tick	Prevalence (% of birds with at least 1 tick)	Total ticks	Ticks/ infested bird (tick load)	Where typically found	Number `weighed	Mean gm	IOC Scientific Name	Authority
Common Yellowthroat	MB	576	39	6.8	49	1.3	G-U	317	10.1	*Geothlypis trichas*	(Linnaeus, 1766)
Grey Catbird	MB	403	14	3.5	18	1.3	G-U	211	35.9	*Dumetella carolinensis*	(Linnaeus, 1766)
American Redstart	MB	332	4	1.2	4	1	Canopy	164	7.7	*Setophaga ruticilla*	(Linnaeus, 1758)
Swamp Sparrow	MB	252	22	8.7	72	3.3	G-U	119	16.0	*Melospiza georgiana*	(Latham, 1790)
American Goldfinch	MB	249	0	0	0		G-U	156	12.5	*Spinus tristis*	(Linnaeus, 1758)
Wilson's Warbler	M	213	1	0.5	2	2	G-U	92	7.7	*Cardellina pusilla*	(Wilson, A, 1811)
Black-capped Chickadee	YR	202	0	0	0		Canopy	131	11.6	*Poecile atricapillus*	(Linnaeus, 1766)
Song Sparrow	MB	185	23	12.4	34	1.5	G-U	98	20.4	*Melospiza melodia*	(Wilson, A, 1810)
American Yellow Warbler	MB	174	0	0	0		G-U	79	9.6	*Setophaga aestiva*	(Gmelin, JF, 1789)
Red-eyed Vireo	MB	165	0	0	0		Canopy	58	17.7	*Vireo olivaceus*	(Linnaeus, 1766)
White-throated Sparrow	M	137	11	8	13	1.2	G-U	66	25.1	*Zonotrichia albicollis*	(Gmelin, JF, 1789)
Nashville Warbler	MB	127	1	0.8	1	1	G-U	58	8.2	*Leiothlypis ruficapilla*	(Wilson, A, 1811)
Red-winged Blackbird	MB	120	2	1.7	3	1.5	G-U	40	57.0	*Agelaius phoeniceus*	(Linnaeus, 1766)
Ruby-crowned Kinglet	M	113	0	0	0		Canopy	53	6.2	*Regulus calendula*	(Linnaeus, 1766)
Myrtle Warbler	M	113	0	0	0		Canopy	69	11.4	*Setophaga coronata*	(Linnaeus, 1766)
House Wren	MB	111	16	14.4	30	1.9	G-U	79	10.7	*Troglodytes aedon*	Vieillot, 1809
Swainson's Thrush	M	108	6	5.6	7	1.2	G-U	57	29.6	*Catharus ustulatus*	(Nuttall, 1840)
White-crowned Sparrow	M	106	2	1.9	2	1	G-U	24	27.7	*Zonotrichia leucophrys*	(Forster, JR, 1772)
Lincoln's Sparrow	M	103	14	13.6	24	1.7	G-U	43	16.9	*Melospiza lincolnii*	(Audubon, 1834)
Palm Warbler	M	98	1	1	1	1	G-U	34	9.7	*Setophaga palmarum*	(Gmelin, JF, 1789)
Alder Flycatcher	MB	89	0	0			Canopy	34	12.7	*Empidonax alnorum*	Brewster, 1895
Northern Waterthrush	MB	86	4	4.7	4	1	G-U	38	32.1	*Parkesia noveboracensis*	(Gmelin, JF, 1789)
Least Flycatcher	MB	73	0	0	0		Canopy	37	17.3	*Empidonax minimus*	(Baird, WM & Baird, SF, 1843)
Cedar Waxwing	MB	61	0	0	0		G-U	44	12.9	*Bombycilla cedrorum*	Vieillot, 1808
Magnolia Warbler	M	59	0	0	0		Canopy	27	8.3	*Setophaga magnolia*	(Wilson, A, 1811)
Ovenbird	MB	59	2	3.4	2	1	G-U	18	18.7	*Seiurus aurocapilla*	(Linnaeus, 1766)
Chipping Sparrow	MB	46	0	0	0		G-U	35	12.0	*Spizella passerina*	(Bechstein, 1798)
Baltimore Oriole	MB	45	0	0	0		Canopy	23	35.1	*Icterus galbula*	(Linnaeus, 1758)
Brown Thrasher	MB	45	6	13.3	23	3.8	G-U	16	74.6	*Toxostoma rufum*	(Linnaeus, 1758)
Eastern Phoebe	MB	39	0	0	0		Canopy	30	18.9	*Sayornis phoebe*	(Latham, 1790)

(Continued on next page)

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Species	Status	Birds examined	Birds with a tick	Prevalence (% of birds with at least 1 tick)	Total ticks	Ticks/ infested bird (tick load)	Where typically found	Number `weighed	Mean gm	IOC Scientific Name	Authority
Canada Warbler	M	39	0	0	0		Canopy	15	10.0	*Cardellina canadensis*	(Linnaeus, 1766)
Grey-cheeked Thrush	M	34	2	5.9	2	1	G-U	19	51.6	*Catharus minimus*	(Lafresnaye, 1848)
Rose-breasted Grosbeak	MB	33	1	3	1	1	G-U	15	45.6	*Pheucticus ludovicianus*	(Linnaeus, 1766)
Blackpoll Warbler	M	31	0	0			Canopy	21	11.6	*Setophaga striata*	(Forster, JR, 1772)
Mourning Warbler	MB	28	1	3.6	1	1	G-U	8	11.9	*Geothlypis philadelphia*	(Wilson, A, 1810)
Indigo Bunting	MB	28	3	10.7	9	3	G-U	13	14.8	*Passerina cyanea*	(Linnaeus, 1766)
Yellow-bellied Sapsucker	MB	27	0	0	0		Canopy	19	48.4	*Sphyrapicus varius*	(Linnaeus, 1766)
Tennessee Warbler	M	27	0	0	0		Canopy	22	9.1	*Leiothlypis peregrina*	(Wilson, A, 1811)
Common Grackle	MB	23	3	13	3	1	G-U	6	94.3	*Quiscalus quiscula*	(Linnaeus, 1758)
Northern Cardinal	YR	22	1	4.5	1	1	G-U	12	43.1	*Cardinalis cardinalis*	(Linnaeus, 1758)
Field Sparrow	MB	22	1	4.5	1	1	G-U	13	12.8	*Spizella pusilla*	(Wilson, A, 1810)
Warbling Vireo	MB	18	0	0	0		Canopy	8	13.3	*Vireo gilvus*	(Vieillot, 1808)
Pine Warbler	M	18	0	0	0		G-U	16	10.9	*Setophaga pinus*	(Linnaeus, 1766)
Orange-crowned Warbler	M	18	0	0	0		G-U	9	8.2	*Leiothlypis celata*	(Say, 1822)
Downy Woodpecker	YR	18	0	0	0		Canopy	14	26.4	*Dryobates pubescens*	(Linnaeus, 1766)
Hairy Woodpecker	YR	14	0	0	0		Canopy	9	40.6	*Leuconotopicus villosus*	(Linnaeus, 1766)
Blue Jay	YR	14	0	0	0		Canopy	7	83.3	*Cyanocitta cristata*	(Linnaeus, 1758)
Northern Flicker	MB	13	0	0	0		Canopy	7	70.3	*Colaptes auratus*	(Linnaeus, 1758)
Scarlet Tanager	MB	13	0	0	0		G-U	8	28.2	*Piranga olivacea*	(Gmelin, JF, 1789)
Yellow-bellied Flycatcher	MB	12	0	0	0		G-U	10	13.5	*Empidonax flaviventris*	(Baird, WM & Baird, SF, 1843)
Cape May Warbler	M	12	0	0	0		Canopy	3	11.9	*Setophaga tigrina*	(Gmelin, JF, 1789)
American Robin	MB	11	0	0	0		Canopy	4	74.3	*Turdus migratorius*	Linnaeus, 1766
Eastern Bluebird	MB	10	0	0	0		Canopy	7	17.2	*Sialia sialis*	(Linnaeus, 1758)
Chestnut-sided Warbler	MB	10	0	0	0		Canopy	3	9.3	*Setophaga pensylvanica*	(Linnaeus, 1766)
Savannah Sparrow	MB	9	0	0	0					*Passerculus sandwichensis*	(Gmelin, JF, 1789)
Red-breasted Nuthatch	MB	9	0	0	0			5	10.1	*Sitta canadensis*	Linnaeus, 1766
Pileated Woodpecker	YR	9	0	0	0			4	11.9	*Dryocopus pileatus*	(Linnaeus, 1758)
Black-throated Green Warbler	MB	7	0	0	0			4	15.4	*Setophaga virens*	(Gmelin, JF, 1789)
Veery	MB	7	2	28.6	2	1		4	7.9	*Catharus fuscescens*	(Stephens, 1817)
Red-bellied Woodpecker	MB	6	0	0	0			4	28.0	*Melanerpes carolinus*	(Linnaeus, 1758)

Purple Finch	MB	6	0	0	0		4	31.8	*Haemorhous purpureus*	(Gmelin, JF, 1789)
Black-and-White Warbler	MB	6	0	0	0		3	9.6	*Mniotilta varia*	(Linnaeus, 1766)
American Woodcock	MB	6	0	0	0				*Scolopax minor*	Gmelin, JF, 1789
Connecticut Warbler	M	5	0	0	0		3	13.3	*Oporornis agilis*	(Wilson, A, 1812)
Blue-headed Vireo	MB	5	0	0	0				*Vireo solitarius*	(Wilson, A, 1810)
Bay-breasted Warbler	M	5	0	0	0		3	30.1	*Setophaga castanea*	(Wilson, A, 1810)
Eastern Towhee	MB	5	1	20	1	1	3	12.2	*Pipilo erythrophthalmus*	(Linnaeus, 1758)
Golden-winged Warbler	MB	4	0	0	0		3	83.0	*Vermivora chrysoptera*	(Linnaeus, 1766)
Hermit Thrush	MB	4	2	50	2	1	3	137.8	*Catharus guttatus*	(Pallas, 1811)
Yellow-throated Vireo	MB	3	0	0	0		3	18.0	*Vireo flavifrons*	Vieillot, 1808
Philadelphia Vireo	M	3	0	0	0		2	77.5	*Vireo philadelphicus*	(Cassin, 1851)
Eastern Wood Pewee	MB	3	0	0	0		2	15.3	*Contopus virens*	(Linnaeus, 1766)
Eastern Kingbird	MB	3	0	0	0		2	20.4	*Tyrannus tyrannus*	(Linnaeus, 1758)
Blue-winged Warbler	M	3	0	0	0		2	51.8	*Vermivora cyanoptera*	Olson & Reveal, 2009
Brown-headed Cowbird	MB	3	0	0	0		1	42.1	*Molothrus ater*	(Boddaert, 1783)
Wood Thrush	MB	2	0	0	0		1	7.1	*Hylocichla mustelina*	(Gmelin, JF, 1789)
White-breasted Nuthatch	MB	2	0	0	0		1	11.1	*Sitta carolinensis*	Latham, 1790
Sharp-shinned Hawk	MB	2	0	0	0		1	79.3	*Accipiter striatus*	Vieillot, 1808
Grasshopper Sparrow	MB	2	0	0	0		1	38.1	*Ammodramus savannarum*	(Gmelin, JF, 1789)
Red Fox Sparrow	M	2	0	0	0		1	20.0	*Passerella iliaca*	(Merrem, 1786)
Clay-colored Sparrow	MB	2	0	0	0		1	31.4	*Spizella pallida*	(Swainson, 1832)
Brown Creeper	MB	2	0	0	0		1	17.5	*Certhia americana*	Bonaparte, 1838
Blackburnian Warbler	MB	2	0	0	0		1	9.8	*Setophaga fusca*	(Müller, PLS, 1776)
Black-billed Cuckoo	MB	2	0	0	0		1	24.8	*Coccyzus erythropthalmus*	(Wilson, A, 1811)
Vesper Sparrow	MB	1	0	0	0		1	24.2	*Pooecetes gramineus*	(Gmelin, JF, 1789)
Dark-eyed Junco	MB	1	0	0	0		1		*Junco hyemalis*	(Linnaeus, 1758)
Orchard Oriole	M	1	0	0	0		1		*Icterus spurius*	(Linnaeus, 1766)
Mourning Dove	MB	1	0	0	0		1		*Zenaida macroura*	(Linnaeus, 1758)
House Finch	MB	1	0	0	0		1		*Haemorhous mexicanus*	(Müller, PLS, 1776)
Great Crested Flycatcher	MB	1	0	0	0		1		*Myiarchus crinitus*	(Linnaeus, 1758)
Eastern Meadowlark	MB	1	0	0	0		1		*Sturnella magna*	(Linnaeus, 1758)
Black-throated Blue Warbler	MB	1	0	0	0		1		*Setophaga caerulescens*	(Gmelin, JF, 1789)
American Tree Sparrow	M	1	0	0	0		1		*Spizelloides arborea*	(Wilson, A, 1810)

Coleoptera Collected Using Three Trapping Methods at Grass River Natural Area, Antrim County, Michigan

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Abstract

Overall, 409 Coleoptera species (369 identified to species, 24 to genus only, and 16 to subfamily only), representing 275 genera and 58 beetle families, were collected from late May through late September 2017 at the Grass River Natural Area (GRNA), Antrim County, Michigan, using baited multi-funnel traps (210 species), pitfall traps (104 species), and sweep nets (168 species). All three collecting methods were used in three distinct habitats: a rich conifer swamp (cedar), near the edge of a red pine plantation (pine), and within a mesic northern hardwood forest (hardwoods). Additional collections were made along two trails and in an open field by sweep netting only. Of the 409 species, 322 were collected in one or more of the cedar, hardwoods, and pine habitats, and 152 were collected along the two trails and the grassland site. Of the 322 species collected in the three main habitats, 40 species (36 genera and 14 families) were collected in all three habitats, 105 species (80 genera and 32 families) were collected in the cedar, 176 (131 genera and 38 families) in the hardwoods, and 199 (158 genera and 47 families) in the pine habitats. With respect to adult seasonal activity, 21% of the 409 species were first collected in May, 40% in June, 23% in July, 10% in August, and 6% in September. Of the 210 species collected in funnel traps, 144, 123, and 114 species were collected, respectively, in traps baited with α-pinene, ethanol, or ipsenol. Diversity indices were calculated for the funnel trap data by site and lure. Overall, 32 of the 409 species were considered exotic to North America, and 18 were considered new state records for Michigan. In addition, 16 species of aquatic beetles (12 genera in 5 families) were identified from GRNA stream samples collected during 2013–2019.

Keywords: beetles, diversity index, state records, funnel trap, pitfall trap, sweep net

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Interest in insect biodiversity and conservation has grown in recent decades along with recognition of the many important ecosystem services that insects provide (Foottit and Adler 2017, Samways 2019). Moreover, recent reports of global insect declines have heightened public awareness of the threats faced by many insects (van Klink et al. 2020). Just over one million species of insects have been described worldwide (Zhang 2011), including nearly 400,000 species of beetles (Coleoptera) (Bouchard et al. 2017). In North America north of Mexico, over 25,000 beetle species have been described (Marske and Ivie 2003), and in Michigan there are about 4000 beetle species recorded (W. G. Ruesink et al., unpublished data).

Beetle surveys in various parts of Michigan have been published since the late 1800s. Schwarz (1876) published one of the first lists based on beetles collected mostly in the Detroit area. Two years later, Hubbard and Schwarz (1878) published a more extensive list (> 2000 species) based on collections in both Michigan's Lower and Upper Peninsulas, including Isle Royale in Lake Superior where they recorded 123 beetle species. Townsend (1889) published a list of beetles (161 species) collected in St. Joseph County, MI. Later, Adams (1909) and Wolcott (1909) added several more species to the list of beetles known to occur on Isle Royale, raising the total to 206 species. Andrews (1916) published an extensive list of beetle species (623 species) found on the Charity Islands in Saginaw Bay, Lake Huron. Andrews (1921) published another long list of beetle species (886 species) found at Whitefish Point in the Upper Peninsula of Michigan. One additional early list of Michigan beetles (580 species) was published by Hatch (1925) for Charlevoix County, including Beaver, Garden and Hog Islands in Lake Michigan. More recently, several authoritative lists of Michigan beetles have been published for specific families or subfamilies, such as Buprestidae (Wellso et al. 1976), Cerambycidae (Gosling 1973, 1983;

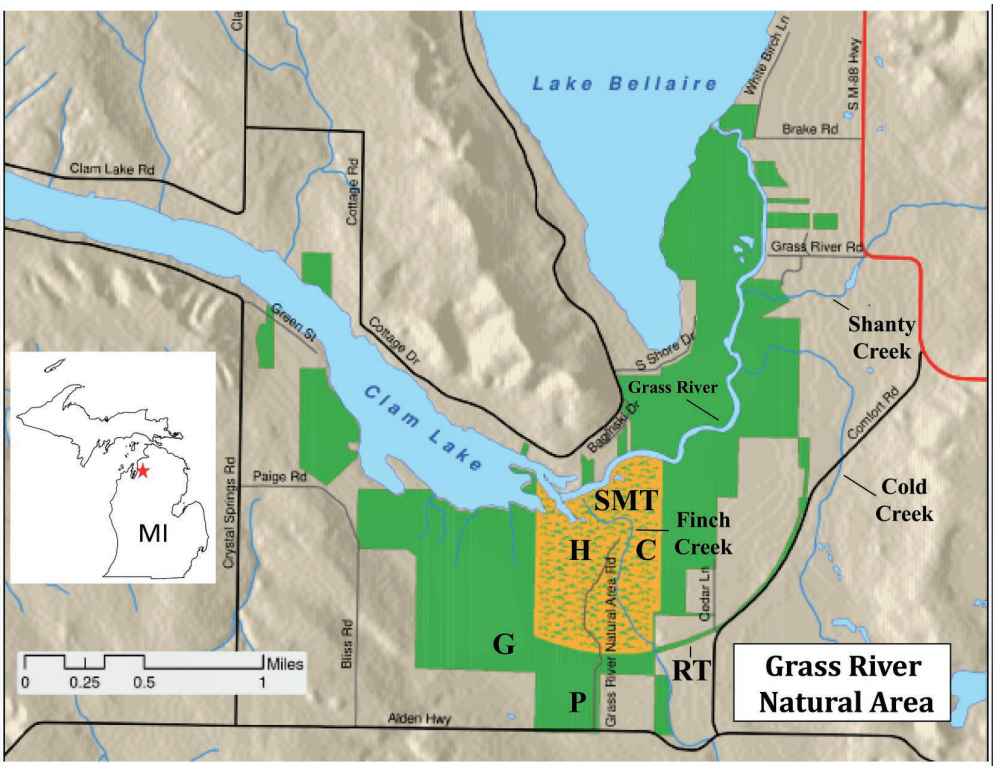

Figure 1. Map of Grass River Natural Area (GRNA), Antrim County, MI, showing all property as of 2020 except for a few parcels at the north end of Lake Bellaire. The green-colored parcels are open to hunting, while the orange-colored area is closed to hunting. Labels for the 2017 sampling sites are: C = cedar habitat, G = grassland, H = hardwoods, P = pine, RT = Rail Trail, and SMT = Sedge Meadow Trail. The three creeks where sampling occurred are marked (Cold, Finch, and Shanty Creeks). The red star inside the inset map of Michigan is the approximate location of GRNA.

Gosling and Gosling 1977), Ciidae (Grey and Cognato 2019), Cleridae (Gosling 1980), Scolytinae (Cognato et al. 2009), Tenebrionidae (Spilman 1973), and several families of aquatic beetles (Bright 2020).

The Grass River Natural Area (GRNA) is in Antrim County in northwestern Lower Michigan, where it straddles much of the Grass River that connects Lake Bellaire to Clam Lake (Fig. 1). GRNA began in 1969 with a single 62 ac (25 ha) parcel and has now expanded to 1492 ac (603 ha), consisting of 73 discrete and mostly contiguous land parcels (GRNA 2020). The staff at GRNA welcomes and supports on-site field research (GRNA 2020).

The Michigan Natural Features Inventory (MNFI) has identified 77 natural community types in Michigan (Kost et al. 2007, Cohen et al. 2015), of which 9 were identified by MNFI staff at GRNA (Hackett et al. 2017). Using MNFI terminology the nine natural communities (habitats) found at GRNA, in decreasing order of size as estimated in 2017, were rich conifer swamp (503 ac; 204 ha), mesic northern forest (283 ac; 115 ha), northern fen (185 ac; 75 ha), poor conifer swamp (82 ac; 33 ha), hardwood-conifer swamp (53 ac; 21 ha), northern wet meadow (49 ac; 20 ha), northern shrub thicket (41 ac; 17 ha), dry-mesic northern forest (30 ac; 12 ha), and emergent marsh (6 ac; 2 ha) (Hackett et al. 2017).

Beetles can be collected in a variety of ways with equipment such as sweep nets, beating sheets, light traps, pitfall traps, baited or unbaited flight-intercept traps, Berlese funnels, and Malaise traps (Dillon and Dillon 1972, White 1983, Evans 2014). In the present study, we used sweep nets, pitfall traps, and baited multi-funnel traps to collect beetles at GRNA in 2017. In this paper, we provide a list of the beetle species

collected with details on their habitat associations, seasonality, methods by which they were collected, and status as being native or exotic to the United States as well as a new state record for Michigan. In addition, diversity indices were calculated for the funnel trap data.

Methods and Materials

Habitats sampled. Trapping and sweep netting was conducted in three GRNA habitats, including rich conifer swamp (which we refer to as "cedar"), mesic northern forest (hardwoods), and along the edge of a mature, red pine (*Pinus resinosa* Sol. ex Aiton) plantation (pine) (Fig. 1). The rich conifer swamp was dominated by northern white cedar (*Thuja occidentalis* L.), with other occasional tree species such as tamarack [*Larix laricina* (Du Roi) K. Koch], balsam fir [*Abies balsamea* (L.) Mill], red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), and black ash (*Fraxinus nigra* Marshall). The mesic northern forest was dominated by hardwood trees such as sugar maple (*Acer saccharum* Marshall) and American beech (*Fagus grandifolia* Ehrh.), with occasional yellow birch, northern red oak (*Quercus rubra* L.), eastern hemlock [*Tsuga canadensis* (L.) Carrière], and white pine (*Pinus strobus* L.). Along the edge of the red pine plantation were occasional red maple, black cherry (*Prunus serotina* Ehrh.), and white pine. A detailed floristic description of each GRNA habitat is given in Hackett et al. (2017). The Latitude-Longitude coordinates of the three main trapping sites were: N 44.9135° Lat and W 85.2186° Long for the cedar site, N 44.9128° Lat and W 85.2246° Long for the hardwood site, and N 44.9050° Lat and W 85.2223° Long for the pine site.

Sweep netting was also conducted along two GRNA trails (Rail Trail and Sedge Meadow Trail) and in an open field (grassland; N 44.9100° Lat and W 85.2333° Long) (Fig. 1). The Rail Trail occurs along the former Pere-Marquette Railway track bed and typically grades on each side from grasses, forbs and shrubs to trees that reflect the adjacent habitats. The Sedge Meadow Trail traverses three habitats: rich conifer swamp, hardwood-conifer swamp, and northern wet meadow. The hardwood-conifer swamp was dominated by northern white cedar, yellow birch, balsam poplar (*Populus balsamifera* L.), and bigtooth aspen (*Populus grandidentata* Michaux), whereas the northern wet meadow was dominated by sedges, grasses, and occasional small shrubs (Hackett et al. 2017).

Sampling methods and frequency. The three main methods of collecting beetles at GRNA involved funnel traps, pitfall traps, and sweep netting. Sampling with funnel traps occurred from 19 May to 24 September 2017, and similarly from 19 May to 22 September 2017 for pitfall traps, and from 23 May to 20 September 2017 for sweep netting. Starting in June or July, respectively, the pitfall traps and funnel traps were "closed" for two weeks each month, usually the first two weeks of each month. Sweep netting occurred at all sites, starting in May or June, and occurred usually two to three times per month, including the trails and grassland site.

Funnel traps. At each of the three main collecting sites, three 12-unit multi-funnel traps (Contech Enterprises Inc., Victoria, British Columbia, Canada) were deployed. The color of the funnels was green as shown in Petrice and Haack (2015). The individual funnels in all traps were coated with Fluon (Northern Products Inc., Woonsocket, RI), a slippery substance that improves trapping efficiency (Graham et al. 2010). The traps were suspended from lower branches of trees so that the bottom of the collection cup was about 1 m above groundline. To make sure the traps were clearly visible to flying insects, any interfering branches were pruned away. The distance between traps at each site ranged from 4–25 m, depending on the location of suitable trees. The collection cup at the bottom of the funnel trap was fitted with a small screen to allow rainwater to drain. Inside each collection cup, a circular piece of window screening was fitted near the bottom that suspended captured insects above any moisture that accumulated at the base of the cup. A few pieces of No-Pest Strip (Spectrum Group, St. Louis, MO), were placed inside each collection cup on top the screen to quickly kill trapped insects. The active ingredient in No-Pest Strips is dichlorvos, an organophosphate insecticide. Three different lures were used at each site, using one lure per trap, including an α-pinene UHR (ultra-high release) pouch with a release rate of 2.3 g per day at 26°C (Alpha Scents, Inc., West Linn, OR), an ethanol UHR pouch with a release rate of about 300 mg per day at 20°C (Contech Enterprises Inc.), and a racemic ipsenol bubble-cap with a release rate of about 0.1–0.2 mg/d at 25°C (Contech Enterprises Inc.). These lures are common attractants to a wide range of bark- and wood-infesting insects and their associates (Miller et al. 2015, Millar and Hanks 2017, Rabaglia et al. 2019). The lures and No-Pest Strips pieces were changed at approximately 6-week intervals. At the end of a sampling period, all insects were removed and placed in a labeled zip-lock plastic bag and frozen until sorted. The collection cup was then cleaned, the screen and No-Pest Strips re-

positioned in the cup, and then the cup was reattached to the trap.

Pitfall traps. Two pitfall traps were installed at the three main collection sites. Each trap consisted of an 18 oz (0.5 l) plastic cup with a ca.10-cm diameter opening that was sunk into the ground so that the top was flush with the soil surface. Two 1-m-long barriers, made from black plastic lawn edging, were partially buried on opposite sides of the cup and positioned flush with the cup's rim at the hardwoods and pine sites, but not the cedar site because the sphagnum surface there was too irregular for the edging to make an effective barrier. Such barriers direct ground invertebrates towards the cup and have been shown to increase trap catch (Durkis and Reeves 1982, Hansen and New 2005, Skvarla et al. 2014). At the start of a sampling period each cup was cleaned and then filled to a depth of ca. 5 cm with 70% ethanol. To reduce dilution from rain, a 25-cm diameter plastic plate was placed ca. 5 cm above each collection cup, supported by large nails. At the end of each sampling period, all beetles were removed and placed in labeled vials with fresh 70% ethanol and then stored until mounted for identification.

Sweep netting. A standard 15-inch (38 cm) diameter heavy duty sweep net with a sailcloth bag was used. Typically, 10-30 min was spent sweeping each site when visited. Most sweeping was conducted on non-woody vegetation, but in each habitat about ten percent of all sweeps consisted of strongly beating the net against woody shrubs and lower tree limbs. The number of sweeps taken was not predetermined and varied with each sampling date, depending on conditions and productivity. The number of sweeps varied among habitats. For example, in the hardwoods habitat only 40–50 sweeps would be taken because there was little appropriate vegetation given that most tree branches were too high to reach with the net and relatively little ground vegetation grew in areas of deep shade. By contrast, as many as 500 sweeps were made in the grassland site where there was about 1 ha of open herbaceous vegetation interspersed with a few shrubs available for sweeping. The beetles collected during sweeping were placed in labeled vials with fresh 70% ethanol and stored until mounted for identification.

Aquatic beetles. In addition to the beetles collected by the methods described above, the authors also examined vials of stored aquatic macroinvertebrates collected by netting in three GRNA creeks (Cold Creek, Finch Creek, and Shanty Creek; Fig. 1) during the spring and fall sampling efforts during 2013-2019. These collections were made by GRNA staff and volunteers as part of the MiCorps Volunteer Stream Monitoring Program, sponsored by Michigan's Department of Environment, Great Lakes, and Energy (https://micorps.net/). Beetles were removed from the stored vials, pinned, labelled, and later identified.

Specimen identification and location. Nearly all beetles were identified by WGR using an AmScope 7X-90X binocular zoom microscope (AmScope, Irvine, CA, USA) and the keys in Downie and Arnett (1996). The identifications were checked against information and photographs on BugGuide (https://bugguide.net/). In cases where some doubt existed regarding the identification, literature suggested on BugGuide as well as the keys in Arnett and Thomas (2001) and Arnett et. al. (2002) were consulted. In addition, for some beetle groups, taxonomic advice and assistance were provided by national experts (see Acknowledgments). The specimens discussed in this paper are currently in the authors' private collections but later a few will be retained at GRNA with the vast majority being deposited in the Michigan State University, Department of Entomology, Albert J. Cook Arthropod Research Collection in East Lansing, MI.

New Michigan state records. The status of each beetle species as being a potential new state record for Michigan was based on data presented in the several authoritative lists of Michigan beetles mentioned in the introduction plus over 350 other publications that have been reviewed in preparation of a formal list of Michigan Coleoptera by W. G. Ruesink et al. Many of these papers mention only one or a few species, but others cover entire major families for all of North America north of Mexico. Examples of the latter include Beal (2003) [Dermestidae], Bousquet (2012) [Carabidae], Bousquet et al. (2018) [Tenebrionidae], Herman (2001) [Staphylinidae, in part], O'Brien and Wibmer (1982) [Curculionidae], Peck and Newton (2017) [Leiodidae], Pelletier and Hébert (2014) [Cantharidae], and Riley et al. (2003) [Chrysomelidae, excluding Bruchinae]. In addition, the online SCAN database (https://scan-bugs.org/) of over 100 North American arthropod collections was consulted to determine if they had Michigan specimens for any of the potential new state records, as well as photographs of identified specimens submitted to BugGuide (https://bugguide.net/) and iNaturalist (https://www.inaturalist.org/) of beetles collected in Michigan. Gary Parsons, Collection Manager of the A. J. Cook Arthropod Research Collection (ARC) at Michigan State University (MSU), was also consulted to check if specimens of any of the potential new state records had recently been deposited in the ARC-MSU collection.

Table 1. Summary data by beetle family for Coleoptera collected at Grass River Natural Area (GRNA) in 2017, including common name of the family and number of species in North America north of Mexico from Evans (2014), number of species and genera collected at GRNA, number of species collected and considered exotic to the United States, habitats where the specimens were collected, methods by which the beetles were collected, and months when collected.

Family	Common name	No. species in North America	No. GRNA species	No. GRNA genera	No. exotic species collected	Habitats where collected[1]	Methods by which collected[2]	Months when collected in 2017[3]
Aderidae	Antlike leaf beetles	48	1	1		HP	F	VI VII IX
Anthicidae	Antlike flower beetles	229	1	1		HP	F	VI VII
Anthribidae	Fungus weevils	88	3	2		GPS	FS	V VI VII VIII IX
Bostrichidae	Bostrichid beetles	77	1	1		P	F	V
Brentidae	Straight-snouted beetles	151	1	1	1	G	S	VII
Buprestidae	Jewel beetles	788	5	4	1	GPS	FS	VI VII VIII IX
Byrrhidae	Moss beetles	57	1	1		H	P	V VI
Cantharidae	Soldier beetles	473	20	7		CGHPSO	FS	V VI VII VIII IX
Carabidae	Ground beetles	2439	41	21	1	CGHPSO	FPS	V VI VII VIII IX
Cerambycidae	Loghorned beetles	958	17	15		CGHPO	FS	V VI VII VIII
Chrysomelidae	Leaf beetles	1869	40	30	4	CGHPSO	FPS	V VI VII VIII IX
Ciidae	Minute tree-fungus beetles	84	1	1		CP	F	VIII IX
Cleridae	Checkered beetles	243	7	6		CHPS	FS	V VI VII VIII IX
Coccinellidae	Lady beetles	481	18	11	2	CGHPSO	FPS	V VI VII VIII IX
Corylophidae	Minute hooded beetles	61	2	2		CHP	F	VI VIII IX
Cryptophagidae	Silken fungus beetles	145	2	2		CP	F	V VI
Curculionidae	Weevils	2919	47	38	13	CGHPSO	FPS	V VI VII VIII IX
Dermestidae	Skin beetles	117	1	1	1	P	F	VI
Elateridae	Click beetles	965	21	11		CGHPSO	FPS	V VI VII VIII
Endomychidae	Handsome fungus beetles	45	2	2		CP	FP	VIII IX
Erotylidae	Pleasing fungus beetles	82	2	2		PS	FS	VI
Eucinetidae	Plate-thigh beetles	11	1	1		H	F	VI
Eucnemidae	False click beetles	85	7	4		HPO	FS	VI VII VIII IX
Geotrupidae	Earth-boring scarab beetles	56	1	1		P	P	VI
Histeridae	Clown beetles	435	3	3		CHP	FP	VI VII VIII IX
Hydrophilidae	Water scavenger beetles	258	2	2		HP	P	VII
Laemophloeidae	Lined flat bark beetles	52	1	1		C	F	VI

Lampyridae	Fireflies	126	7	6		CGHPSO	FPS	V VI VII VIII IX
Latridiidae	Minute brown scavenger beetles	140	5	3		CGHPS	FS	V VI VII VIII IX
Leiodidae	Round fungus beetles	381	3	2		CP	FP	V VI VIII IX
Lucanidae	Stag beetles	25	1	1		HP	F	VI
Lycidae	Net-winged beetles	76	3	2		PO	FS	VII VIII IX
Melandryidae	False darkling beetles	50	4	4		CHP	F	VI VII VIII IX
Meloidae	Blister beetles	424	1	1		O	S	VII
Melyridae	Soft-winged flower beetles	520	4	3		GPO	FS	VI VII VIII
Monotomidae	Root-eating beetles	56	1	1		HP	F	VI VII
Mordellidae	Tumbling flower beetles	189	9	3		CGHPSO	FS	V VI VII VIII IX
Mycetophagidae	Hairy fungus beetles	26	1	1		CGHPS	FS	V VI VIII IX
Nemonychidae[4]	Pine flower snout beetles	15	1	1		P	F	V
Nitidulidae	Sap beetles	173	6	4		CHP	FP	V VI VII VIII IX
Oedemeridae	False blister beetles	87	1	1		CP	F	V VI
Phalacridae	Shining flower beetles	122	4	3		GHSO	S	VI VII VIII IX
Ptiliidae	Featherwing beetles	117	1	1		C	P	IX
Ptilodactylidae	Ptilodactylid beetles	19	1	1		CS	FPS	VI VII
Ptinidae	Deathwatch & spider beetles	471	3	3		CHP	F	V VI VII VIII IX
Pyrochroidae	Fire-colored beetles	50	1	1		H	F	VI
Scarabaeidae	Scarab beetles	1700	20	14	4	CGHPO	FPS	V VI VII VIII IX
Scirtidae	Marsh beetles	50	8	5		CGHPSO	FS	V VI VII VIII IX
Scraptiidae	False flower beetles	46	3	2		CHP	F	V VI VII
Silphidae	Carrion beetles	30	4	3		CHP	FP	VI VII VIII IX
Silvanidae	Silvanid flat bark beetles	32	2	2		HP	F	VI VII
Sphindidae	Cryptic slime mold beetles	9	1	1		H	F	VI
Staphylinidae	Rove beetles	4360	43	20	5	CHPO	FPS	V VI VII VIII IX
Tenebrionidae	Darkling beetles	1184	13	8		CGHPSO	FPS	V VI VII VIII IX
Tetratomidae	Polypore fungus beetles	26	2	2		H	F	VII VIII IX
Throscidae	Throscid beetles	20	3	2		HP	F	V VI VIII
Trogossitidae	Bark-gnawing beetles	59	2	2		CP	F	VI VII
Zopheridae	Zopherid beetles	109	2	2		HP	F	V VI

[1] Habitats: C = cedar, G = grassland, H = hardwoods, O = other, but primarily the Rail Trail, P = pine, and S = Sedge Meadow Trail. See text for details.

[2] Methods: F = funnel traps, P = pitfall traps, and S = sweeping.

[3] Months: V = May, VI = June, VII = July, VIII = August, and IX = September, X = October.

[4] Some sources have elevated certain subfamilies of Nemonychidae to family status, such as Cimberidinae being elevated to Cimberidae.

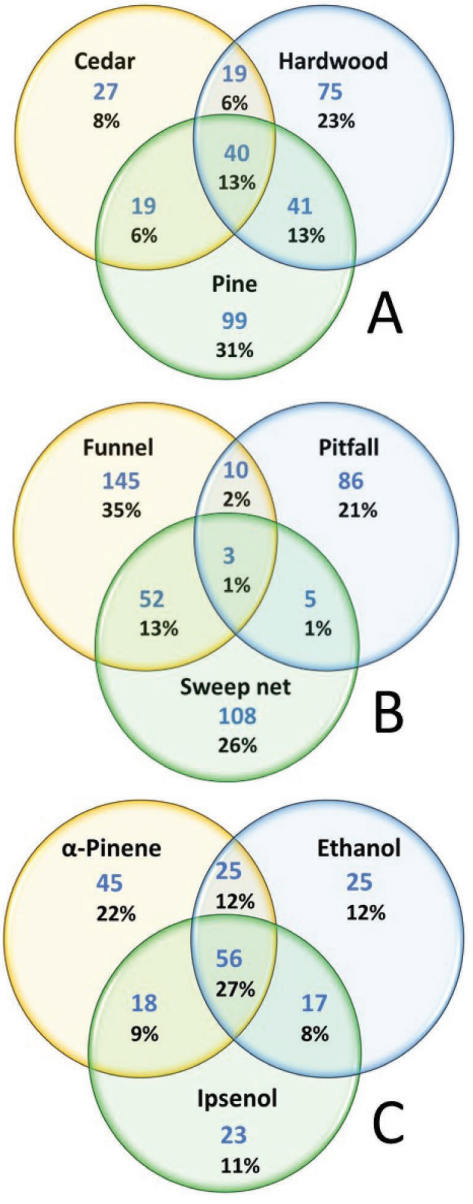

Figure 2. Venn diagrams indicating the number of beetle species and corresponding percent of the total for A: the 322 species that were collected in the cedar, hardwoods, and pine habitats (the label of one specimen was lost so the numbers add to 321); B: the 409 species that were collected in funnel traps, pitfall traps, and by sweep netting; and C: the 210 species that were collected in funnel traps baited with either α-pinene, ethanol, or ipsenol (values add to 209 due to one lost label).

Status as native or exotic. As above, notes were recorded for each species as to whether they were native or exotic to the United States. The main sources of information were again Downie and Arnett (1996) and the internet site BugGuide. The native range of the exotic species was described as Asian, Eurasian, European, or Palearctic (northern portion of Eurasia).

Diversity indices. Several diversity indices have been used in ecological studies to characterize community diversity, with some, such as the Shannon index, combining species richness (i.e., the total number of different species) and the proportion of each species into a single value (Washington 1984, Chao et al. 2014). Using EstimateS (Colwell 2013), we calculated the Shannon index (H) and the effective (or equivalent) number of species [ENS = exp(H)] values for the funnel trap data given that the total number of each beetle species collected was recorded from all traps. We computed separate values for each of the three main habitats (cedar, hardwoods, and pine) by combining all funnel trap data (i.e., from the three different lures) within each habitat, and also for each of the three lures (α-pinene, ethanol, or ipsenol) by combining the funnel trap data by lure type across the three habitats. The ENS value is calculated as the exponential of the Shannon index, exp(H), and is equivalent to the number of equally common species required to produce the same diversity index value (Jost 2006). For example, Shannon index values of 2, 3, 4, and 5 would be equivalent to communities with 7, 20, 55, and 148 equally common species, respectively.

Results

For all three collecting methods combined, 409 beetle species were identified from the 2017 GRNA samples, including 369 taxa identified to species, 24 to genus only, and 16 to subfamily only (Appendix 1). These 409 species represented 58 families, with the five most speciose being Curculionidae (47 species), Staphylinidae (43), Carabidae (41), Chrysomelidae (40), and Elateridae (21) (Table 1). By contrast, there were 20 families represented by only a single species, and another 22 families represented by only 2-5 species each (Table 1). There was a significant positive linear correlation between the number of species collected per beetle family at GRNA and the corresponding total number of North American species (north of Mexico) recognized in those same families, using the values presented in Table 1 and Evans (2014) (r = 0.91, R^2 = 0.83, N = 58, P < 0.0001). The 40 taxa that were not identified to species represented 16 beetle families, 22 of which were Staphylinidae, and 16 of

Table 2. Number of families, genera, and species of beetles collected at Grass River Natural Area in 2017 in the cedar, hardwoods, and pine habitats by trapping method (funnel traps, pitfall traps, and sweep netting); see text for details.

	No. families, genera, species by trapping method		
Habitat	**Funnel traps**	**Pitfall traps**	**Sweep net**
Cedar	30, 63, 78	10, 23, 34	11, 18, 24
Hardwoods	34, 98, 116	11, 38, 57	10, 27, 38
Pine	43, 118, 140	14, 41, 53	19, 47, 53

the 22 staphylinids were only identified to the subfamily Aleocharinae (Appendix 1).

Habitats. Of the 409 species collected at GRNA, 322 were collected at the three main sampled habitats (cedar, hardwoods, and pine) using all three trapping methods, compared with 152 species being collected by sweeping along the two GRNA trails and the grassland site (Appendix 1). Of the 322 species, 105 species (80 genera in 32 families) were collected in the cedar habitat, 176 species (131 genera in 38 families) in the hardwoods habitat, and 199 species (158 genera in 47 families) in the pine habitat (Appendix 1). Similarly, of these 322 species and the three main habitats sampled, 27 species were collected only in the cedar habitat, 76 only in the hardwoods habitat, and 99 only in the pine habitat, whereas 40 species were collected in all three habitats (Fig. 2a). For the three GRNA locations where only sweep netting occurred, 57 beetle species (47 genera in 18 families, including 16 unique species) were collected along the Sedge Meadow Trail, 69 species (56 genera in 18 families, including 18 unique species) along the Rail Trail, and 83 species (67 genera in 19 families, including 36 unique species) in the grassland site (Appendix 1).

Trapping methods. Of the 409 species collected in this study, 210 species (165 genera in 51 families) were collected in funnel traps, 104 species (66 genera in 20 families) in pitfall traps, and 168 species (124 genera in 26 families) with sweep nets (Fig. 2b, Appendix 1). Similarly, the greatest number of species were collected in funnel traps when considering the cedar, hardwoods, and pine habitats separately (Table 2). Of the 409 species, 145 species were collected only with funnel traps, 86 species only with pitfall traps, and 108 species only with sweep nets (Fig. 2b). By contrast, only three species were collected with all three methods (Fig. 2b), including the carabid *Calathus gregarious* (Say), the coccinellid *Brachiacantha decempustulata* (Melsheimer), and a ptilodactylid *Ptilodactyla* sp. (Appendix 1).

Lures. Of the 210 species collected in funnel traps, 144 species (119 genera in 39 families) were collected in funnel traps baited with α-pinene, 123 species (97 genera in 36 families) in ethanol-baited traps, and 114 species (97 genera in 38 families) in ipsenol-baited traps (Fig. 2c, Appendix 1). Of these 210 species, 45 species were collected only with α-pinene, 25 species only with ethanol, and 23 species only with ipsenol (Fig. 2c). By contrast, 56 species were collected with all three lures (Fig. 2c). The label was lost on one specimen and thus the values in Fig. 2c only add to 209, not 210. Considering all collections made from the nine funnel traps used in 2017, 707 individual beetles were collected in the three funnel traps baited with α-pinene lures, 513 individuals in the three traps with ethanol lures, and 553 individuals in the three traps with ipsenol lures (Appendix 1). When combining the funnel trap data at each site, 79 beetle species were collected at the cedar site, 116 at the hardwoods site, and 143 at the pine site. Several beetle species showed a strong preference for one of the three lures tested. For example, α-pinene was most attractive to the curculionid *Pissodes affinis* Randall (capturing 96% of 23 individuals) and the histerid *Paromalus bistriatus* Erichson (95% of 20), ethanol was most attractive to the curculionid *Anisandrus sayi* Hopkins (97% of 72) and the nitidulid *Glischrochilus sanguinolentus* (Olivier) (93% of 27), and ipsenol was most attractive to the cerambycid *Monochamus scutellatus* (Say) (61% of 66) and the clerid *Madoniella dislocata* (Say) (73% of 108) (Appendix 1).

Diversity indices. The Shannon index values H, based on funnel trap data only, were 3.297 for the cedar habitat, 3.971 for the hardwoods habitat, and 4.075 for the pine habitat. The corresponding effective number of equally common species (ENS) for these Shannon index values are 27 for cedar, 53 for hardwoods, and 59 for pine. Similarly, considering the three lures tested, the Shannon Index values H were 4.314 for the α-pinene, 4.005 for ethanol, and 3.764 for

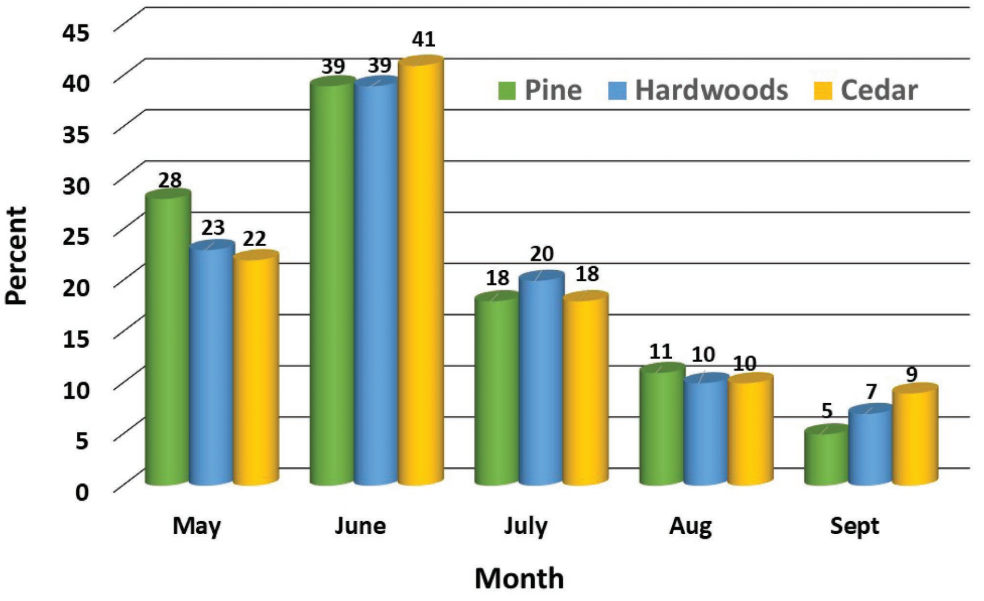

Figure 3. Percentage of beetle species collected by three sampling methods at Grass River Natural Area in 2017 by month of first collection and habitat for the beetle species collected in the cedar (105 species), hardwoods (176 species), and pine (199 species) habitats. Values above each column are percentage values within each habitat.

ipsenol, which correspond to ENS values of 75, 55, and 43, respectively.

Seasonality. Of the 409 beetle species collected at GRNA in 2017, 21% (85 species) were first collected in May, 40% (162) in June, 23% (95) in July, 10% (41) in August, and 6% (26) in September (Appendix 1). A broadly similar pattern emerged for each of the three main habitats sampled, with most species being first collected in May or June (Fig. 3). Moreover, when considering just those beetle species collected in funnel traps, the resulting season-long species accumulation curves for each of the three main habitats were similar in shape with more species consistently being collected at the pine site compared with the hardwoods and cedar sites (Fig. 4). At the family level, 48% (28 families) of the 58 beetle families recorded were first collected in May, 38% (22) in June, 9% (5) in July, 3% (2) in August, and 2% (1) in September (Table 1). The two beetle families first collected in August were Ciidae and Endomychidae, with members of Ptiliidae being first collected in September (Table 1). Considering the number of beetle species collected each month for all 409 species, 21% (85 species) were collected in May, 59% (243) in June, 46% (187) in July, 33% (133) in August, and 27% (111) in September (Appendix 1).

New Michigan state records. Of the 369 species that were identified to the species level, we found published, in print, collection records from Michigan for 336 species. For the remaining 33 species, 14 were listed online in SCAN as having been collected in Michigan and deposited in the Albert J. Cook Arthropod Research Collection at Michigan State University (1 of the 14 was also deposited in the C.A. Triplehorn Insect Collection at The Ohio State University), 1 was listed on BugGuide as having been collected in Michigan, and the remaining 18 were considered new state records for Michigan (Appendix 1). These 18 new state records are members of 12 beetle families, including Brentidae (1 species), Cantharidae (2), Chrysomelidae (4), Cryptophagidae (1), Curculionidae (3), Hydrophilidae (1), Laemophloeidae (1), Melyridae (1), Silvanidae (1), Staphylinidae (1), Tenebrionidae (1), and Throscidae (1) (Appendix 1). Four of these 18 species are exotic to the United States, including the brentid *Perapion curtirostre* (Germar), the chrysomelids *Chrysolina hyperici* (Forster) and *Mantura chrysanthemi* (Koch), and the staphylinid *Tasgius melanarius* (Heer).

Status as native or exotic. Overall, 32 of the beetle species collected at GRNA were exotic to the United States (Appendix 1). These 32 species represent 9 beetle

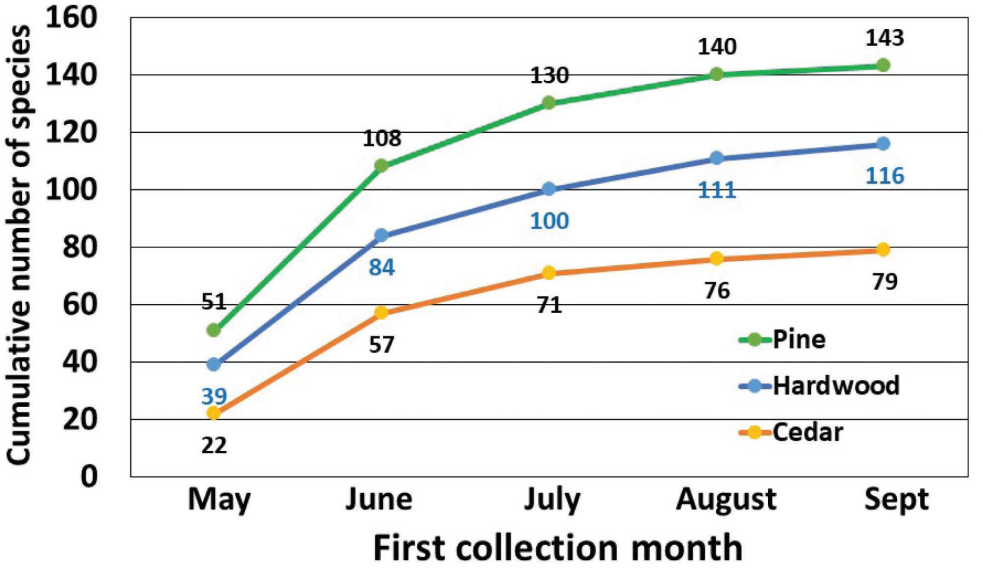

Figure 4. Cumulative number of species collected in funnel traps (all lures combined within sites) by month in three habitats (cedar, hardwoods, and pine) sampled during May to September 2017 at Grass River Natural Area.

families, including Brentidae (1 species), Buprestidae (1), Carabidae (1), Chrysomelidae (4), Coccinellidae (2), Curculionidae (13), Dermestidae (1), Scarabaeidae (4), and Staphylinidae (5). The natural range of these 32 exotics was Asia for 4 species, Europe for 12, Eurasia for 5, and the Palearctic for 11 (Appendix 1).

Aquatic beetles. Examination of the invertebrates from the stored GRNA stream samples from 2013–2019 revealed 16 species of adult aquatic beetles, representing 12 genera in 5 families (Table 3). Of these 16 species, 11 were identified to the species level and 5 to genus only (Table 3). Overall, there were 4 species of Dytiscidae, 1 Elmidae, 3 Gyrinidae, 2 Haliplidae, and 6 Hydrophilidae. All taxa identified to species are considered native to the United States and none were new state records for Michigan. Aquatic beetles were collected from each of the three creeks sampled at GRNA, including Cold Creek, Finch Creek, and Shanty Creek (Table 3, Fig. 1).

Discussion

Although over 400 beetle species were collected at GRNA in 2017, this number undoubtedly represents only a fraction of the total number of beetle species present. Insect diversity tends to increase with sampling intensity in insect surveys (Samways et al. 2010). As an example, consider the work of Muona (1999), who used large numbers of pitfall traps and flight-intercept traps in three separate studies at Oulanka National Park in Finland, where the beetle fauna is very well known, but reported collecting only 54-61% of the known terrestrial beetle species present in each study. If these same ratios are applied to our GRNA data (409 species), then the total number of terrestrial beetle species at GRNA would be estimated at 670–757 species. Still we would postulate that there would be even more beetle species present at GRNA than these estimates given that sampling intensity in Muona's (1999) studies involved 100–240 pitfall traps and 32–120 flight-intercept traps, depending on the study. Additionally, sampling over successive years typically results in more species being discovered at any site. To demonstrate this point, consider the 10-year study by Martikainen and Kaila (2004) in Finland that focused on saproxylic beetles (those species dependent on dead or decaying wood; Ulyshen and Šobotník 2018) at two forest sites. They reported that only 50% of all 258 saproxylic species collected over the entire 10-year study were collected every single year, that many species showed great year-to-year variation in population size (as reflected in trap catch numbers), and that new species were collected in every year of the study.

Our single-year trapping effort focused on just three habitats, using three

Table 3. Species of aquatic beetles collected during 2013-2019 in three creeks that cross Grass River Natural Area, including Cold Creek, Finch Creek, and Shanty Creek (see text for details and Fig. 1 for creek locations).

FAMILY **Subfamily** **Species**	**Creek name (number collected, date)**
DYTISCIDAE (Predaceous diving beetles)	
Agabinae	
Ilybiosoma seriatum (Say)	Shanty (3, 16 V 2015), Shanty (1, 3 X 2015);
Agabus sp.	Finch (1, 28 IX 2019)
Hydroporinae	
Liodessus crotchi Nilsson	Finch (1, 27 IX 2014), Cold (1, 17 X 2017)
Neoporus sp.	Cold (2, 16 V 2015), (Shanty (1, 16 V 2015)
ELMIDAE (Riffle beetles)	
Elminae	
Dubiraphia bivittata (LeConte)	Shanty (1, 16 V 2015)
GYRINIDAE (Whirligig beetles)	
Gyrininae	
Gyrinus maculiventris LeConte	Cold (1, 27 IX 2014)
Gyrinus lecontei Fall	Finch (3, 28 IX 2019)
Gyrinus sp.	Cold (1, 6 V 2017), Shanty (2, 21 V 2014)
HALIPLIDAE (Crawling water beetles)	
Haliplus canadensis (Wallis)	Cold (1, 16 V 2015)
Haliplus immaculicollis Harris	Cold (1, 16 V 2015)
HYDROPHILIDAE (Water scavenger beetles)	
Hydrophilinae	
Anacaena lutescens (Stephens)	Cold (2, 16 V 2015)
Enochrus ochraceus (Melsheimer)	Shanty (2, 16 V 2015)
Hydrobius fuscipes (Linnaeus)	Shanty (1, 16 V 2015)
Hydrobius melaenus (Germar)	Shanty (2, 3 X 2015)
Paracymus sp.	Cold (1, 12 X 2013)
Tropisternus sp.	Finch (6, 12 X 2013)

sampling methods and deploying only three funnel traps and two pitfall traps per site. We recognize that many more beetle species would have been collected at GRNA if we had sampled in multiple years, started sampling earlier and ended later in the year, sampled more habitats, deployed more traps per site, used a greater variety of baits in the funnel traps, sampled at different heights within the canopy, and sampled over multiple years. In addition, many more beetle species would have been collected if we had used additional methods, such as flight-intercept window-pane traps, light traps, Malaise traps, and Berlese funnels. Nevertheless, our modest trapping effort did document about 10% of the beetle species known to occur in Michigan, given that Michigan has around 4000 recognized beetle species (W. G. Ruesink et al., unpublished data).

Of the three collection methods used in the present study, baited funnel traps caught the greatest number of beetle species, whereas pitfall traps caught the fewest (Fig. 2b). Multiple collection methods have been compared in many other studies. At forested sites in Finland, Hyvärinen et al. (2006) found that two types of flight-intercept traps caught a greater number of beetle species than did pitfall traps. Similarly, in a forested area of Arkansas, Skvarla and Dowling (2017) compared 12 trapping methods for collecting four groups of beetles (Carabidae, Buprestidae, Cerambycidae, and Curculionoidea excluding Scolytinae) and found that the best trapping method varied by beetle family. For example, the greatest diversity of buprestids was collected in Malaise traps and unbaited green funnel traps; whereas Malaise traps, canopy SLAM traps, and

funnel traps were best for cerambycids; pitfall traps and funnel traps were best for non-scolytine curculionoids; and pitfall traps were best for carabids. In the present study, 33 (80%) of the 41 carabid species collected at GRNA were collected in pitfall traps, compared with only 4 carabid species in funnel traps and 6 species in sweep-net samples (Appendix 1).

The three lures used in the present study are commonly used in surveys for bark- and wood-infesting beetles, especially Cerambycidae and Scolytinae (Brockerhoff et al. 2006, Millar and Hanks 2017, Rabaglia et al. 2019, Rassati et al. 2019). In fact, since 2007 the USDA Forest Service has implemented a nationwide survey for exotic bark and ambrosia beetles, using funnel traps baited with α-pinene, ethanol and a three-component pheromone lure containing ipsdienol, cis-verbenol, and methyl-butenol (Rabaglia et al. 2019). As noted in the present study, Miller et al. (2015) and Rabaglia et al. (2019) also reported that many cerambycid and scolytine species showed strong preferences for individual lures similar to the lures we tested, either individually or in various combinations.

Volatile compounds such as α-pinene and ethanol are often produced at increased levels in stressed trees, and thus many bark- and wood-infesting insects have evolved to use these compounds to locate stressed host plants (Mattson and Haack 1987, Millar and Hanks 2017). Besides cerambycids and scolytines, many other beetles use α-pinene and ethanol, as well as bark beetle pheromones, as kairomones to locate stressed plants (e.g., some Bostrichidae, Buprestidae, and Nitidulidae) or potential prey (e.g., some Cleridae, Histeridae, and Tenebrionidae) (Chénier and Philogène 1989, Schroeder and Lindelöw 1989, Erbilgin and Raffa 2002, Bouget et al. 2009, Millar and Hanks 2017).

Variation in seasonal adult activity among insects reflects their overwintering life stage, overwintering site, and voltinism pattern (Wolda 1988). In temperate areas, many insects overwinter as larvae (Danks 1978), and thus must still complete metamorphosis before adult activity can begin. Many others overwinter as adults and are thus most abundant in late spring or in late summer and autumn. Adults of temperate insects tend to have one of three seasonal patterns: a single peak, multiple peaks (for multivoltine species), or one broad maximum (Wolda 1988). Although we collected new beetle species at GRNA in all months from May to September, June had the greatest number (162 of 409) of new species collected for any single month. Similar seasonal patterns have been reported by others for Coleoptera. For example, in New Zealand, using Malaise traps, Hutcheson (1990) noted that both insect species richness and abundance increased from spring to summer and then declined into fall. In Arkansas, using multiple trapping methods, Skvarla and Dowling (2017) noted different adult activity patterns among different groups of beetles: Carabidae were active from spring to fall with a slight peak in June, Buprestidae and Cerambycidae were most active in June and July, and Curculionoidea (excluding Scolytinae) were most active in May and June. In the present study, we had similar results for members of these same beetle groups with most species initiating adult activity in June (Appendix 1).

Shannon index (H) values have been reported in dozens of Coleoptera survey studies, but usually with a focus on just one or a few beetle families. However, all Coleoptera families and species were included in the analyses of a few studies and therefore can be compared to our results for the cedar (H = 3.297; ENS = 27), hardwoods (H = 3.971, ENS = 53), and pine sites (H = 4.075, ENS = 59). For example, Coulson et al. (1971), working in North Carolina, reported diversity values for the canopy Coleoptera collected in a monoculture stand of white pine (seasonal range of H = 0.969–2.205, ENS = 3–9) and a mostly oak-hickory (*Quercus-Carya*) forest (seasonal range of H = 1.931–2.941, ENS = 7–19). Trieff (2002), working at multiple sites in Tennessee, collected canopy Coleoptera by fogging northern red oak trees and reported a range in season-long H values of 3.04 to 3.70 (ENS = 21–40) for the various sites. In a third study, working in a mixed-conifer forest in California, Apigian et al. (2006) reported an overall H value of 3.73 (ENS = 42) for all Coleoptera collected in pitfall traps collected over a 3-year period.

Faunistic surveys provide basic knowledge on the occurrence, abundance and distribution of selected species within a given area. To that end, the present study provides information on over 400 beetle species found at the Grass River Natural Area in Antrim County, Michigan, and will serve as a baseline for future surveys of Coleoptera in Michigan.

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Appendix 1. Coleoptera collected at Grass River Natural Area in 2017, using funnel traps (F) and pitfall traps (P), and by sweeping (S), with details on habitats where specimens were collected, months when collected, and numbers of individuals collected in funnel traps by bait type. Additional information is presented on whether each species is considered a potential new state record for Michigan (species with an * after the species name), and if each species is considered native or exotic to the continental USA.

FAMILY Subfamily Species[1]	Habitats[2]	Months collected[3]	Methods[4]	Funnel trap collections[5]				Native to USA[6]
				a-p	ETOH	Ips	Total	
ADERIDAE								
Elonus basalis (LeConte)	HP	VI VII IX	F	3	1	0	4	Yes
ANTHICIDAE								
Notoxinae								
Notoxus desertus Casey	HP	VI VII	F	7	4	1	12	Yes
ANTHRIBIDAE								
Anthribinae								
Euparius marmoreus (Olivier)	P	V VI VII VIII	F	2	3	0	5	Yes
Trigonorhinus rotundatus (LeConte)	G	VII	S	0	0	0	0	Yes
Trigonorhinus sticticus (Boheman)	GS	VI IX	S	0	0	0	0	Yes
BOSTRICHIDAE								
Bostrichinae								
Prostephanus punctatus (Say) ‡	P	V	F	1	0	0	1	Yes
BRENTIDAE								
Apioninae								
***Perapion curtirostre* (Germar) ***	G	VII	S	0	0	0	0	Eur
BUPRESTIDAE								
Agrilinae								
Agrilus cuprescens (Ménétriés)	GS	VII	S	0	0	0	0	Pal
Agrilus politus (Say)	G	VI VII	S	0	0	0	0	Yes
Taphrocerus gracilis (Say)	GPS	VII VIII IX	S	0	0	0	0	Yes
Buprestinae								
Anthaxia inornata (Randall)	G	VI	S	0	0	0	0	Yes
Chrysochroinae								
Dicerca divaricata (Say)	P	VI	F	2	0	0	2	Yes
BYRRHIDAE								
Byrrhinae								
Cytilus alternatus (Say)	H	V VI	P	0	0	0	0	Yes

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Appendix 1. Continued.

FAMILY Subfamily Species[1]	Habitats[2]	Months collected[3]	Methods[4]	Funnel trap collections[5] a-p	ETOH	Ips	Total	Native to USA[6]
CANTHARIDAE								
Cantharinae								
Atalantycha bilineata (Say)	G	V	S	0	0	0	0	Yes
Atalantycha neglecta (Fall) ‡	HP	V VI	F	4	2	1	7	Yes
Cantharis tuberculata (LeConte)	GPS	VI	S	0	0	0	0	Yes
Dichelotarsus piniphilus (Eschscholtz)	S	VII	S	0	0	0	0	Yes
Podabrus brevicollis Fall ‡	HO	VI	FS	1	1	1	3	Yes
Podabrus diadema (Fabricius)	G	VIII	S	0	0	0	0	Yes
Podabrus frater LeConte	GHS	VI VII	S	0	0	0	0	Yes
Podabrus rugosulus LeConte	G	VI	S	0	0	0	0	Yes
Podabrus tricostatus (Say)	CH	VI	FS	1	1	0	2	Yes
Rhagonycha fraxini (Say)	O	VII	S	0	0	0	0	Yes
***Rhagonycha hirticula* (Green) ***	SO	VI	S	0	0	0	0	Yes
Rhagonycha imbecillis (LeConte) ‡	HSO	VII VIII	S	0	0	0	0	Yes
Rhagonycha nanula (LeConte)	S	VII	S	0	0	0	0	Yes
Rhagonycha oriflava (LeConte)	G	VI	S	0	0	0	0	Yes
Rhagonycha recta (Melsheimer)	CHP	VI VII VIII	FS	3	1	1	5	Yes
Rhagonycha scitula (Say)	S	VII	S	0	0	0	0	Yes
***Rhagonycha septentrionis* (Green) ***	G	VII	S	0	0	0	0	Yes
Rhagonycha vilis (LeConte)	CHP	VI VII VIII IX	F	25	8	1	34	Yes
Chauliognathinae								
Chauliognathus pensylvanicus (DeGeer)	GO	VIII IX	S	0	0	0	0	Yes
Silinae								
Polemius canadensis Brown	S	VII	S	0	0	0	0	Yes
CARABIDAE								
Carabinae								
Carabus goryi Dejean	P	V VIII	P	0	0	0	0	Yes
Sphaeroderus stenostomus lecontei Dejean	CP	V VIII	P	0	0	0	0	Yes
Harpalinae								
Agonum fidele Casey	H	VI VIII	P	0	0	0	0	Yes
Agonum gratiosum (Mannerheim)	S	IX	S	0	0	0	0	Yes
Amara angustata (Say)	H	VI	P	0	0	0	0	Yes
Amara ellipsis (Casey)	P	VII	P	0	0	0	0	Yes
Amphasia interstitialis (Say)	H	IX	P	0	0	0	0	Yes
Anisodactylus agricola (Say)	H	VI	P	0	0	0	0	Yes
Anisodactylus kirbyi Lindroth	P	VI	P	0	0	0	0	Yes

Calathus gregarius (Say)	PO	VI VII VIII IX	FPS	1	0	2	3	Yes
Calleida punctata LeConte	G	VI	S	0	0	0	0	Yes
Cyclotrachelus sodalis (LeConte)	P	VI VII	P	0	0	0	0	Yes
Cymindis americana Dejean	P	VIII	P	0	0	0	0	Yes
Cymindis limbata Dejean	CHP	V VI VII VIII	F	2	3	4	9	Yes
Cymindis platicollis (Say)	P	VI	F	2	1	0	3	Yes
Dromius piceus Dejean	CHP	V VI	F	3	4	2	9	Yes
Harpalus erythropus Dejean	P	V	P	0	0	0	0	Yes
Harpalus providens Casey	P	VII	P	0	0	0	0	Yes
Harpalus somnulentus Dejean	HP	VI VII VIII IX	P	0	0	0	0	Yes
Lebia fuscata Dejean	P	VII	S	0	0	0	0	Yes
Lebia viridis Say	GO	VI VIII	S	0	0	0	0	Yes
Myas cyanescens Dejean	P	VI VII	P	0	0	0	0	Yes
Platynus decentis (Say)	H	VI	P	0	0	0	0	Yes
Poecilus lucublandus (Say)	H	VI VIII IX	P	0	0	0	0	Yes
Pterostichus adstrictus Eschscholtz	H	VI	P	0	0	0	0	Yes
Pterostichus commutabilis (Motschulsky)	H	VI	P	0	0	0	0	Yes
Pterostichus coracinus (Newman)	C	VII VIII	P	0	0	0	0	Yes
Pterostichus corvinus (Dejean)	CH	VI	P	0	0	0	0	Yes
Pterostichus luctuosus (Dejean)	H	IX	P	0	0	0	0	Yes
Pterostichus melanarius (Illiger)	H	VI VII IX	P	0	0	0	0	Eur
Pterostichus mutus (Say)	CP	VIII	P	0	0	0	0	Yes
Pterostichus stygicus (Say)	CHP	VIII IX	P	0	0	0	0	Yes
Pterostichus tristis (Dejean)	O	VI	S	0	0	0	0	Yes
Selenophorus opalinus (LeConte)	P	VI	P	0	0	0	0	Yes
Synuchus impunctatus (Say)	HP	VII VIII IX	P	0	0	0	0	Yes
Trechinae								
Bembidion affine Say	H	V	P	0	0	0	0	Yes
Bembidion fortestriatum (Motschulsky)	H	IX	P	0	0	0	0	Yes
Bembidion mimus Hayward	H	IX	P	0	0	0	0	Yes
Bembidion semicinctum Notman	H	VII VIII	P	0	0	0	0	Yes
Bembidion sp.	H	VII	P	0	0	0	0	NA
Trechus apicalis Motschulsky	HP	VII VIII IX	P	0	0	0	0	Yes
CERAMBYCIDAE								
Cerambycinae								
Neoclytus acuminatus (Fabricius)	C	VII	F	0	1	0	1	Yes
Xylotrechus sagittatus (Germar)	H	VII	F	0	1	0	1	Yes
Xylotrechus undulatus (Say)	CHP	VI VII	F	6	2	1	9	Yes
Lamiinae								
Astylopsis sexguttata (Say)	CG	VI VII	FS	1	0	0	1	Yes

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Appendix 1. Continued.

FAMILY Subfamily Species[1]	Habitats[2]	Months collected[3]	Methods[4]	Funnel trap collections[5] a-p	ETOH	Ips	Total	Native to USA[6]
Monochamus scutellatus (Say)	CHP	VI VII	F	21	5	40	66	Yes
Oberea tripunctata (Swederus)	G	VII	S	0	0	0	0	Yes
Pogonocherus mixtus Haldeman	P	VIII	S	0	0	0	0	Yes
Saperda mutica Say	G	VI	S	0	0	0	0	Yes
Tetraopes melanurus Schoenherr	G	VII	S	0	0	0	0	Yes
Tetraopes tetrophthalmus (Forster)	G	VIII	S	0	0	0	0	Yes
Lepturinae								
Analeptura lineola (Say)	O	VI	S	0	0	0	0	Yes
Brachyleptura champlaini Casey	G	VIII	S	0	0	0	0	Yes
Grammoptera haematites (Newman)	P	VI	F	1	0	0	1	Yes
Strangalepta abbreviata (Germar)	O	VI	S	0	0	0	0	Yes
Typocerus velutinus (Olivier)	PO	VII	FS	1	0	0	1	Yes
Spondylidinae								
Asemum striatum (Linnaeus)	CHP	V VI	F	4	0	1	5	Yes
Tetropium cinnamopterum Kirby	H	V	F	1	0	0	1	Yes
CHRYSOMELIDAE								
Bruchinae								
Bruchus brachialis Fåhraeus	G	VI VIII	S	0	0	0	0	Pal
Cassidinae								
Chalepus walshii (Crotch)	G	VI VII VIII IX	S	0	0	0	0	Yes
Microrhopala vittata (Fabricius)	O	VI VIII	S	0	0	0	0	Yes
Sumitrosis inaequalis (Webar)	O	IX	S	0	0	0	0	Yes
Chrysomelinae								
Calligrapha multipunctate (Say)	GO	VI VIII	S	0	0	0	0	Yes
Chrysolina hyperici (Forster) #	GPS	VI	S	0	0	0	0	EurAs
Chrysomela knabi Brown	O	VII	S	0	0	0	0	Yes
Chrysomela mainensis Bechyne	S	V	S	0	0	0	0	Yes
Gonioctena americana (Schaeffer)	PO	V VI VII	FS	0	1	3	4	Yes
Labidomera clivicollis (Kirby)	GS	VII	S	0	0	0	0	Yes
Cryptocephalinae								
Bassareus mammifer (Newman)	CPO	VI VIII	FS	0	6	0	6	Yes
Cryptocephalus quadruplex Newman	P	VI	S	0	0	0	0	Yes
Cryptocephalus venustus Fabricius	G	VIII	S	0	0	0	0	Yes
Diachus auratus (Fabricius)	GS	VII VIII	S	0	0	0	0	Yes
Exema canadensis Pierce	GO	VII VIII IX	S	0	0	0	0	Yes
Lexiphanes saponatus (Fabricius)	S	VII VIII	S	0	0	0	0	Yes

Neochlamisus comptoniae (Brown)	G	VIII	S	0	0	0	0	Yes
Neochlamisus eubati (Brown)	GSO	VII VIII IX	S	0	0	0	0	Yes
Pachybrachis othonus (Say)	G	VII	S	0	0	0	0	Yes
Pachybrachis trinotatus (Melsheimer)	G	VII VIII	S	0	0	0	0	Yes
Donaciinae								
Donacia tuberculifrons Schaeffer	SO	VI	S	0	0	0	0	Yes
Plateumaris rufa (Say)	CHO	V VI	FS	1	2	0	3	Yes
Eumolpinae								
Paria fragariae Wilcox ‡	GHO	VI VII VIII IX	PS	0	0	0	0	Yes
Paria pratensis Balsbaugh	HO	VIII IX	S	0	0	0	0	Yes
Paria thoracica (Melsheimer) ‡	HO	IX	S	0	0	0	0	Yes
Xanthonia decemnotata (Say)	HP	V VI VII	FS	6	5	58	69	Yes
Xanthonia villosula (Melsheimer)	GPO	VIII XI	FS	0	0	1	1	Yes
Galerucinae								
***Altica gloriosa* Blatchley ***	S	VI IX	S	0	0	0	0	Yes
Capraita subvittata (Horn)	S	VI	S	0	0	0	0	Yes
***Crepidodera longula* Horn ***	GPS	VI VII	S	0	0	0	0	Yes
Crepidodera nana (Say)	GPS	V VI VII VIII	FS	4	1	4	9	Yes
Crepidodera populivora Parry	P	VI	F	0	1	0	1	Yes
Crepidodera violacea Melsheimer	P	V	F	7	2	0	9	Yes
Diabrotica undecimpunctata howardi Barber	G	IX	S	0	0	0	0	Yes
***Luperaltica nigripalpis* (LeConte) ***	GPO	VII VIII IX	FS	1	0	0	1	Yes
***Mantura chrysanthemi* (Koch) ***	G	VI	S	0	0	0	0	Eur
Neogalerucella sp.	S	VI VII	S	0	0	0	0	Pal
Ophraella conferta (LeConte)	GHO	VI VIII IX	S	0	0	0	0	Yes
Tricholochmaea decora (Say)	G	VI	S	0	0	0	0	Yes
Trirhabda borealis Blake	G	VII	S	0	0	0	0	Yes
CIIDAE								
Ciinae								
Cis fuscipes Mellié	CP	VIII IX	F	1	0	1	2	Yes
CLERIDAE								
Clerinae								
Enoclerus nigrifrons (Say)	CH	VI VII IX	F	7	1	0	8	Yes
Enoclerus nigripes rufiventris (Spinola)	CHP	V VI VII IX	F	17	9	3	29	Yes
Thanasimus dubius (Fabricius)	CHP	V VI VII VIII IX	F	20	10	20	50	Yes
Epiphloeinae								
Madoniella dislocata (Say)	CHP	VII VIII IX	F	7	22	79	108	Yes
Hydnocerinae								
Phyllobaenus pallipennis (Say)	P	VIII IX	FS	6	0	0	6	Yes

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Appendix 1. Continued.

FAMILY Subfamily Species[1]	Habitats[2]	Months collected[3]	Methods[4]	Funnel trap collections[5] a-p	ETOH	Ips	Total	Native to USA[6]
Thaneroclerinae								
Zenodosus sanguineus (Say)	C	VIII	F	0	1	0	1	Yes
Tillinae								
Cymatodera bicolor (Say)	S	VII	S	0	0	0	0	Yes
COCCINELLIDAE								
Chilocorinae								
Chilocorus stigma (Say)	PS	V	FS	0	0	1	1	Yes
Coccinellinae								
Anatis labiculata (Say)	P	VI	F	1	0	0	1	Yes
Anatis mali (Say)	O	VIII	S	0	0	0	0	Yes
Anisosticta bitriangularis (Say)	S	VII VIII	S	0	0	0	0	Yes
Coccinella monticola Mulsant	O	VI	S	0	0	0	0	Yes
Coccinella septempunctata Linnaeus	G	VI VII VIII	S	0	0	0	0	EurAs
Coccinella trifasciata perplexa Mulsant	GPO	V VI VII VIII IX	FS	4	0	5	9	Yes
Cycloneda munda (Say)	GS	VI VII VIII IX	S	0	0	0	0	Yes
Harmonia axyridis (Pallas)	GPS	V VI VII VIII	FS	15	1	3	19	Asian
Hippodamia parenthesis (Say)	G	VI VII VIII IX	S	0	0	0	0	Yes
Psyllobora vigintimaculata (Say)	PO	VI IX	FS	1	0	0	1	Yes
Scymninae								
Brachiacantha decempustulata (Melsheimer)	GPO	VI VII VIII	FPS	2	0	1	3	Yes
Brachiacantha quadripunctata Melsheimer ‡	G	VIII	S	0	0	0	0	Yes
Hyperaspis binotata (Say)	CGPSO	V VI VII VIII IX	FS	15	2	4	21	Yes
Hyperaspis proba (Say)	GP	VII VIII IX	FS	0	1	0	1	Yes
Hyperaspis undulata (Say)	G	VIII	S	0	0	0	0	Yes
Scymnus rubricaudus Casey	P	VII	S	0	0	0	0	Yes
Scymnus sp.	H	V	F	1	0	0	1	NA
CORYLOPHIDAE								
Corylophinae								
Clypastraea lunata (LeConte)	CH	VI VIII IX	F	2	2	0	4	Yes
Sericoderus lateralis (Gyllenhal)	HP	VI VIII	F	1	1	0	2	Yes
CRYPTOPHAGIDAE								
Cryptophaginae								
Atomaria sp.	P	VI	F	1	0	0	1	NA
***Henoticus mycetoecus* (Park) ***	C	V	F	0	1	0	1	Yes

CURCULIONIDAE								
Baridinae								
Dirabius rectirostris (LeConte)	GO	VII	S	0	0	0	0	Yes
Odontocorynus salebrosus (Casey)	GO	VI VIII	S	0	0	0	0	Yes
Odontocorynus umbellae (Fabricius)	G	VIII	S	0	0	0	0	Yes
***Sibariops sectator* Casey ***	O	V	S	0	0	0	0	Yes
Stethobaris ovata (LeConte)	H	VIII	F	1	0	0	1	Yes
Ceutorhynchinae								
Rhinoncus castor (Fabricius)	G	VI	S	0	0	0	0	Pal
Conoderinae								
Acoptus suturalis LeConte	HP	V VI	F	1	1	0	2	Yes
Cossoninae								
***Trichacorynus protractus* (Horn) ***	C	VI	P	0	0	0	0	Yes
Curculioninae								
Anthonomus subfasciatus LeConte	P	VI	F	1	0	0	1	Yes
Orchestes pallicornis (Say)	P	V	F	0	1	0	1	Yes
Rhinusa tetra (Fabricius)	G	VI	S	0	0	0	0	Eur
Tachyerges ephippiatus Say	GPS	VI IX	FS	0	1	0	1	Yes
Tachyerges salicis (Linnaeus)	P	VI	F	0	0	1	1	Yes
Tychius picirostris (Fabricius)	C	VI	F	1	0	0	1	Eur
Dryophthorinae								
Dryophthorus americanus Bedel	C	VII	FP	1	0	0	1	Yes
***Sphenophorus scoparius* Horn ***	H	VI	P	0	0	0	0	Yes
Entiminae								
Barypeithes pellucidus (Boheman)	CHP	VI VII	P	0	0	0	0	Eur
Mesagroicus minor Buchanan	P	VIII	P	0	0	0	0	Yes
Otiorhynchus ovatus (Linnaeus)	HPO	VI VII	PS	0	0	0	0	EurAs
Otiorhynchus rugosostriatus (Goeze)	HO	VII VIII	PS	0	0	0	0	Eur
Otiorhynchus sulcatus (Fabricius)	HO	VII VIII IX	PS	0	0	0	0	Eur
Phyllobius oblongus (Linnaeus)	GHP	V VI VII	FS	4	5	2	11	Pal
Polydrusus formosus (Mayer)	GHPO	V VI VII VIII IX	FS	7	1	1	9	Eur
Sciaphilus asperatus (Bonsdorff)	GHSO	VII VIII IX	S	0	0	0	0	Eur
Sitona cylindricollis (Fåhraeus)	O	VII	S	0	0	0	0	Pal
Sitona lineellus (Bonsdorff)	G	VI	S	0	0	0	0	Yes
Mesoptiliinae								
Magdalis gentilis LeConte	GP	VI	FS	1	0	0	1	Yes
Molytinae								
Conotrachelus nenuphar (Herbst)	H	VI	F	0	2	0	2	Yes
Conotrachelus posticatus Boheman	HP	VIII IX	P	0	0	0	0	Yes
Hylobius congener Dalla Torre et al.	CHP	VI VII	FP	5	0	2	7	Yes

(Continued on next page)

Appendix 1. Continued.

FAMILY Subfamily Species[1]	Habitats[2]	Months collected[3]	Methods[4]	Funnel trap collections[5] a-p	ETOH	Ips	Total	Native to USA[6]
Pissodes affinis Randall	HP	V VI VII	F	22	1	0	23	Yes
Pissodes approximatus Hopkins	CHP	V VI	F	5	0	0	5	Yes
Rhyssomatus lineaticollis (Say)	GP	VI	FS	0	0	1	1	Yes
Scolytinae								
Anisandrus obesus (LeConte)	H	VI VII	F	0	17	0	17	Yes
Anisandrus sayi Hopkins	CHP	V VI VII IX	F	1	70	1	72	Yes
Corthylus punctatissimus (Zimmermann)	P	VI VII IX	FP	0	2	0	2	Yes
Crypturgus borealis Swaine	CH	V VI VII VIII	F	7	2	8	17	Yes
Dryocoetes autographus (Ratzeburg)	CHP	VI VII VIII IX	F	2	5	0	7	Yes
Gnathotrichus materiarius (Fitch)	CHP	V VI VII VIII IX	F	3	1	4	8	Yes
Ips grandicollis (Eichhoff)	HP	V VI	F	14	1	2	17	Yes
Ips pini (Say)	CH	V VI VII VIII IX	F	6	2	6	14	Yes
Lymantor decipiens (LeConte)	HP	VIII IX	F	0	0	2	2	Yes
Monarthrum mali (Fitch)	HP	V VI	F	2	2	0	4	Yes
Orthotomicus caelatus (Eichhoff)	CP	V VI VII	F	2	3	4	9	Yes
Phloeotribus liminaris (Harris)	HP	V VI VII	F	2	41	1	44	Yes
Xyleborinus saxeseni (Ratzeburg)	CHP	VI VII VIII	F	1	5	0	6	EurAs
Xylosandrus germanus (Blandford)	CHP	V VI VII IX	FP	4	11	3	18	Asian
DERMESTIDAE								
Megatominae								
Anthrenus verbasci (Linnaeus)	P	VI	F	1	0	1	2	Eur
ELATERIDAE								
Cardiophorinae								
Cardiophorus convexulus LeConte	HP	V VI	F	15	6	1	22	Yes
Cardiophorus convexus (Say)	CHP	V VI VII	FP	31	14	12	57	Yes
Cardiophorus gagates Erichson	CHPO	V VI VII	FS	21	4	0	25	Yes
Dendrometrinae								
Athous acanthus (Say)	PO	VII VIII	FS	1	0	0	1	Yes
Athous brightwelli (Kirby)	P	V VII	F	3	0	0	3	Yes
Elathous discalceatus (Say)	CHP	VII VIII	F	0	1	3	4	Yes
Gambrinus plebejus (Say)	CHP	V VI	F	3	11	6	20	Yes
Hemicrepidius memnonius (Herbst)	P	V VII	F	0	1	1	2	Yes
Limonius basilaris (Say)	O	VI	S	0	0	0	0	Yes
Pseudanostirus hieroglyphicus (Say)	CP	V VI	F	5	1	2	8	Yes
Pseudanostirus propolus (LeConte)	P	VII	S	0	0	0	0	Yes

Pseudanostirus triundulatus (Randall)	CH	V VI	F	1	2	2	5	Yes
Elaterinae								
Ampedus mixtus (Herbst)	CHPS	V VI VII	FS	3	10	6	19	Yes
Ampedus pedalis Germar	CHS	V VI VII	FS	3	10	10	23	Yes
Dalopius vagus Brown ‡	HPSO	V VI VII VIII	FS	0	2	1	3	Yes
Dalopius vernus Brown ‡	S	V	S	0	0	0	0	Yes
Elater abruptus Say	HP	VI VII	F	4	1	0	5	Yes
Melanotus castanipes (Paykull)	CHP	V VI VII VIII	F	20	6	22	48	Yes
Melanotus communis-complex	CHP	V VI VII	FS	7	6	3	16	Yes
Melanotus hyslopi Van Zwaluwenberg	CHPO	VI VII VIII	FS	1	1	2	4	Yes
Melanotus sp.	G	VI	S	0	0	0	0	NA
ENDOMYCHIDAE								
Leiestinae								
Phymaphora pulchella Newman	C	VIII IX	F	1	0	2	3	Yes
Lycoperdininae								
Lycoperdina ferruginea LeConte	P	IX	P	0	0	0	0	Yes
EROTYLIDAE								
Languriinae								
Acropteroxys gracilis (Newman)	S	VI	S	0	0	0	0	Yes
Erotylinae								
Triplax frosti Casey	P	VI	F	0	1	0	1	Yes
EUCINETIDAE								
Eucinetus strigosus LeConte	H	VI	F	1	0	0	1	Yes
EUCNEMIDAE								
Macraulacinae								
Onichodon canadensis (Brown)	H	VII VIII IX	F	0	0	3	3	Yes
Melasinae								
Dirrhagofarsus ernae Otto, Muona & McClarin	H	VI	F	3	2	1	6	Yes
Entomophthalmus rufiolus (LeConte)	HP	VII VIII IX	F	0	2	2	4	Yes
Microrhagus carinicollis Otto	H	VI	F	2	1	0	3	Yes
Microrhagus pectinatus LeConte	H	VI VII	F	1	0	0	1	Yes
Microrhagus subsinuatus LeConte	HP	VI	F	1	3	1	5	Yes
Microrhagus triangularis (Say)	PO	VII VIII IX	FS	0	0	2	2	Yes
GEOTRUPIDAE								
Bolboceratinae								
Odonteus sp.	P	VI	P	0	0	0	0	NA

(Continued on next page)

Appendix 1. Continued.

FAMILY Subfamily Species[1]	Habitats[2]	Months collected[3]	Methods[4]	Funnel trap collections[5]				Native to USA[6]
				a-p	ETOH	Ips	Total	
HISTERIDAE								
Dendrophilinae								
Paromalus bistriatus Erichson	CH	VI VII VIII IX	F	19	0	1	20	Yes
Histerinae								
Atholus sedecimstriatus (Say)	H	IX	F	0	0	1	1	Yes
Saprininae								
Euspilotus assimilis (Paykull)	P	VIII	P	0	0	0	0	Yes
HYDROPHILIDAE								
Hydrophilinae								
***Chaetarthria atra* (LeConte) ***	H	VII	P	0	0	0	0	Yes
Helocombus bifidus (LeConte)	P	VII	P	0	0	0	0	Yes
LAEMOPHLOEIDAE								
***Laemophloeus fervidus* Casey ***	C	VI	F	0	0	1	1	Yes
LAMPYRIDAE								
Lampyrinae								
Ellychnia corrusca (Linnaeus)	CGHPSO	V VI VIII IX	FS	13	10	30	53	Yes
Lucidota atra (Olivier)	HSO	VI	FS	1	0	0	1	Yes
Photinus indictus (LeConte)	G	VI	S	0	0	0	0	NA
Photinus sp.	CGHPO	VI VII	FS	5	2	2	10	Yes
Pyractomena angulata (Say)	S	VI	S	0	0	0	0	Yes
Pyropyga decipiens (Harris)	CGHSO	VI VII VIII	PS	0	0	0	0	Yes
Photurinae								
Photuris sp.	HSO	VI	S	0	0	0	0	NA
LATRIDIIDAE								
Corticariinae								
Corticaria sp.	CP	VI	F	2	1	1	4	NA
Melanophthalma americana (Mannerheim)	GPS	VIII IX	FS	2	0	0	2	Yes
Melanophthalma distinguenda (Comolli)	CHP	V VI VII VIII	F	19	15	20	54	Yes
Melanophthalma pumila (LeConte)	C	V	F	0	0	1	1	Yes
Latridiinae								
Stephostethus liratus (LeConte)	HPS	V VI VIII IX	FS	3	0	7	10	Yes
LEIODIDAE								
Cholevinae								
Catops basilaris Say	P	V	P	0	0	0	0	Yes

Leiodinae								
Leiodes assimilis (LeConte)	P	VII IX	FP	0	1	1	2	Yes
Leiodes punctostriata Kirby	CP	VI VIII IX	P	0	0	0	0	Yes
LUCANIDAE								
Syndesinae								
Ceruchus piceus (Weber)	HP	VI	F	0	0	3	3	Yes
LYCIDAE								
Calochrominae								
Calochromus perfacetus (Say)	P	VII	S	0	0	0	0	Yes
Lycinae								
Calopteron reticulatum (Fabricius)	PO	VII VIII	FS	0	1	1	2	Yes
Calopteron terminale (Say)	O	IX	S	0	0	0	0	Yes
MELANDRYIDAE								
Melandryinae								
Dircaea liturata LeConte	P	VII	F	1	0	1	2	Yes
Orchesia castanea Melsheimer	HP	VI VIII IX	F	4	3	1	8	Yes
Rushia longula (LeConte)	H	VII	F	0	1	0	1	Yes
Serropalpus substriatus Haldeman	CH	VI VIII	F	9	2	4	15	Yes
MELOIDAE								
Nemognathinae								
Nemognatha nemorensis Hentz	O	VII	S	0	0	0	0	Yes
MELYRIDAE								
Malachiinae								
***Attalus frosti* Marshall ***	O	VI	S	0	0	0	0	Yes
Attalus terminalis (Say)	GPO	VI VII	S	0	0	0	0	Yes
Collops quadrimaculatus (Fabricius)	GP	VI VII VIII	S	0	0	0	0	Yes
Hypebaeus sp.	P	VI	F	0	0	2	2	NA
MONOTOMIDAE								
Rhizophaginae								
Rhizophagus remotus LeConte	HP	VI VII	F	0	1	2	3	Yes
MORDELLIDAE								
Mordellinae								
Mordella atrata Melsheimer	CGPSO	VI VII	FS	0	1	1	2	Yes
Mordella marginata Melsheimer	P	VIII	F	0	1	0	1	Yes
Mordella melaena Germar	P	VI IX	F	2	0	0	2	Yes
Mordellistena fuscipennis (Melsheimer)	P	VII	F	1	0	0	1	Yes

(Continued on next page)

Appendix 1. Continued.

FAMILY Subfamily Species[1]	Habitats[2]	Months collected[3]	Methods[4]	Funnel trap collections[5]				Native to USA[6]
				a-p	ETOH	Ips	Total	
Mordellistena pulchra Liljeblad	CP	VI VII	F	0	1	1	2	Yes
Mordellistena tosta LeConte	H	VII	S	0	0	0	0	Yes
Mordellistena trifasciata (Say)	CP	VII	F	2	1	0	3	Yes
Mordellistena vera Liljeblad	CS	VII	FS	0	1	0	1	Yes
Mordellochroa scapularis (Say)	P	V	F	0	0	1	1	Yes
MYCETOPHAGIDAE								
Mycetophaginae								
Litargus tetraspilotus LeConte	CGHPS	V VI VIII IX	FS	17	3	7	27	Yes
NEMONYCHIDAE[7]								
Cimberidinae								
Cimberis elongata (LeConte)	P	V	F	0	0	1	1	Yes
NITIDULIDAE								
Carpophilinae								
Carpophilus brachypterus (Say)	P	V	F	2	1	0	3	Yes
Carpophilus lugubris Murray ‡	CHP	IX	P	0	0	0	0	Yes
Cryptarchinae								
Glischrochilus sanguinolentus (Olivier)	CHP	V VI VII VIII IX	FP	1	25	1	27	Yes
Glischrochilus siepmanni W. J. Brown	C	IX	P	0	0	0	0	Yes
Nitidulinae								
Stelidota geminata (Say) ‡	CHP	VII VIII IX	P	0	0	0	0	Yes
Thalycra concolor (LeConte)	CHP	VI VII VIII IX	FP	1	0	6	7	Yes
OEDEMERIDAE								
Oedemerinae								
Asclera ruficollis (Say)	CP	V VI	F	3	2	1	6	Yes
PHALACRIDAE								
Eustilbinae								
Acylomus ergoti Casey	H	VIII	S	0	0	0	0	Yes
Olibrinae								
Olibrus semistriatus LeConte	G	VII	S	0	0	0	0	Yes
Phalacrinae								
Phalacrus politus Melsheimer	SO	VI VII VIII IX	S	0	0	0	0	Yes
Phalacrus sp.	S	VII	S	0	0	0	0	NA

PTILIIDAE								
Ptiliinae								
Ptiliola sp.	C	IX	P	0	0	0	0	NA
PTILODACTYLIDAE								
Ptilodactylinae								
Ptilodactyla sp.	CS	VI VII	FPS	1	0	0	1	NA
PTINIDAE								
Anobiinae								
Hadrobregmus notatus (Say)	HP	V VI	F	4	0	7	11	Yes
Priobium sericeum (Say)	H	VII VIII IX	F	0	1	3	4	Yes
Dorcatominae								
Sculptotheca puberula (LeConte)	C	VII VIII IX	F	0	1	2	3	Yes
PYROCHROIDAE								
Pyrochroinae								
Neopyrochroa flabellata (Fabricius)	H	VI	F	0	0	1	1	Yes
SCARABAEIDAE								
Aphodiinae								
Aegialia criddlei Brown ‡	H	VI	P	0	0	0	0	Yes
Colobopterus erraticus (Linnaeus)	H	VI IX	F	1	0	1	2	Pal
Dialytes striatulus (Say)	H	VII	F	1	0	1	2	Pal
Dialytes truncatus (Melsheimer)	P	VII	F	0	0	1	1	Yes
Pseudagolius bicolor (Say)	P	IX	F	1	0	0	1	Yes
Melolonthinae								
Dichelonyx albicollis Burmeister	P	V VI VII	FS	2	1	2	5	Yes
Dichelonyx backii Kirby	CHP	V	F	0	1	2	3	Yes
Dichelonyx elongatula (Schönherr)	O	VI	S	0	0	0	0	Yes
Diplotaxis sordida (Say)	P	V VI	FP	6	0	0	6	Yes
Hoplia trifasciata Say	P	V	F	1	1	0	2	Yes
Macrodactylus subspinosus (Fabricius)	GPO	VI VII	FS	2	2	0	4	Yes
Phyllophaga crenulata (Froelich)	P	VI	F	1	0	0	1	Yes
Phyllophaga nitida (LeConte)	C	VII	F	1	0	0	1	Yes
Phyllophaga sp. 1	HP	V VI	F	0	1	1	2	Yes
Phyllophaga sp. 2	P	VI	F	0	0	1	1	NA
Serica spp.	HP	V VI VII	F	32	18	16	66	NA
Rutelinae								
Popillia japonica Newman	GO	VII IX	S	0	0	0	0	Asian
Scarabaeinae								
Copris minutus (Drury)	P	VIII	P	0	0	0	0	Asian

(Continued on next page)

Appendix 1. Continued.

FAMILY Subfamily Species[1]	Habitats[2]	Months collected[3]	Methods[4]	Funnel trap collections[5]				Native to USA[6]
				a-p	ETOH	Ips	Total	
Melanocanthon nigricornis (Say)	P	VI	P	0	0	0	0	Yes
Onthophagus hecate (Panzer)	CP	VI VIII	P	0	0	0	0	Yes
SCIRTIDAE								
Scirtinae								
Contacyphon neopadi (Klausnitzer) ‡	SO	VII	S	0	0	0	0	Yes
Contacyphon obscurus (Guérin-Méneville)	CHPS	V VI VII VIII	FS	13	4	7	24	Yes
Contacyphon variabilis (Thunberg)	CHPSO	V VI VII VIII IX	FS	42	3	20	65	NA
Contacyphon unnamed nr. obscurus	CHS	V VI VII	FS	9	4	4	17	Yes
Nyholmia confusa (Brown)	GS	VII	S	0	0	0	0	Yes
Prionocyphon limbatus LeConte ‡	GHO	VI VII VIII IX	FS	8	4	6	18	Yes
Sacodes thoracica (Guérin-Méneville)	HP	V VI VIII	F	0	1	2	3	Yes
Scirtes tibialis Guérin-Méneville	HSO	VII IX	FS	0	1	1	2	Yes
SCRAPTIIDAE								
Anaspidinae								
Anaspis flavipennis Haldeman	HP	V VI	F	4	0	1	5	Yes
Anaspis rufa Say	C	VI	F	0	0	1	1	Yes
Scraptiinae								
Canifa pallipes (Melsheimer)	CHP	VI VII	F	1	3	3	7	Yes
SILPHIDAE								
Nicrophorinae								
Nicrophorus orbicollis Say	HP	VI IX	FP	0	1	3	4	Yes
Nicrophorus sayi Laporte	C	VI	F	0	0	1	1	Yes
Silphinae								
Necrophila americana (Linnaeus)	HP	VI VII VIII	P	0	0	0	0	Yes
Oiceoptoma noveboracense (Forster)	HP	VII	P	0	0	0	0	Yes
SILVANIDAE								
Brontinae								
Telephanus velox (Haldeman)	P	VI	F	1	0	0	1	Yes
Silvaninae								
***Silvanus muticus* Sharp ***	H	VII	F	0	1	0	1	Yes
SPHINDIDAE								
Sphindinae								
Sphindus americanus LeConte	H	VI	F	1	0	0	1	Yes

STAPHYLINIDAE								
Aleocharinae								
Aleochara lata Gravenhorst	H	IX	F	0	0	1	1	Pal
Aleochara sp.	H	VI	P	0	0	0	0	NA
Unknown sp. 1	P	VIII	F	1	0	0	1	NA
Unknown sp. 2	P	VIII IX	P	0	0	0	0	NA
Unknown sp. 3	O	IX	S	0	0	0	0	NA
Unknown sp. 4	P	IX	P	0	0	0	0	NA
Unknown sp. 5	CH	VII	P	0	0	0	0	NA
Unknown sp. 6	H	VII IX	P	0	0	0	0	NA
Unknown sp. 7	H	VII	P	0	0	0	0	NA
Unknown sp. 8	C	VIII IX	P	0	0	0	0	NA
Unknown sp. 9	P	IX	P	0	0	0	0	NA
Unknown sp. 10	HP	IX	P	0	0	0	0	NA
Unknown sp. 11	H	VII	P	0	0	0	0	NA
Unknown sp. 12	CP	IX	P	0	0	0	0	NA
Unknown sp. 13	H	VII IX	P	0	0	0	0	NA
Unknown sp. 14	CH	VIII	P	0	0	0	0	NA
Unknown sp. 15	C	VIII	P	0	0	0	0	NA
Unknown sp. 16	H	VII	P	0	0	0	0	NA
Omaliinae								
Eusphalerum orientale (Bernhauer)	P	V VI	F	1	2	1	4	Yes
Phloeostiba lapponicus (Zetterstedt)	HP	VI IX	F	5	1	0	6	Yes
Oxytelinae								
Oxytelus laqueatus (Marsham)	label lost	VI	F	0	0	0	1	Pal
Paederinae								
Paederus littorarius Gravenhorst	H	VII	P	0	0	0	0	Pal
Palaminus sp.	C	VII	F	1	0	0	1	NA
Pselaphinae								
Batrisodes sp.	C	IX	P	0	0	0	0	NA
Scaphidiinae								
Baeocera sp.	HP	VI VII	F	1	1	0	2	NA
Staphylininae								
Belonuchus rufipennis (Fabricius)	H	VI	F	1	0	0	1	Yes
Bisnius blandus (Gravenhorst)	CH	VII IX	P	0	0	0	0	Yes
Dinothenarus badipes (LeConte)	CH	VI VII VIII IX	P	0	0	0	0	Yes
Nudobius cephalus (Say)	P	VI	F	1	0	0	1	Yes
Ontholestes cingulatus (Gravenhorst)	H	VIII	P	0	0	0	0	Yes
Philonthus caeruleipennis (Mannerheim)	C	VII	P	0	0	0	0	Yes
Quedius fulgidus (Fabricius)	C	IX	P	0	0	0	0	Yes

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Appendix 1. Continued.

FAMILY Subfamily Species[1]	Habitats[2]	Months collected[3]	Methods[4]	Funnel trap collections[5]				Native to USA[6]
				a-p	ETOH	Ips	Total	
Quedius fulvicollis (Stephens)	P	VIII	P	0	0	0	0	Yes
Quedius laticollis (Gravenhorst)	HP	VIII IX	P	0	0	0	0	Yes
Quedius peregrinus (Gravenhorst)	CP	VIII IX	P	0	0	0	0	Yes
Quedius plagiatus Mannerheim	H	VIII	F	0	1	0	1	Yes
Quedius sp.	P	VII	P	0	0	0	0	NA
Tasgius melanarius (Heer) *	H	IX	P	0	0	0	0	EurAs
Tachyporinae								
Carphacis sp.	P	VI	F	0	1	0	1	NA
Sepedophilus littoreus (Linnaeus)	H	VI	F	1	0	0	1	Eur
Tachinus fimbriatus Gravenhorst	CP	VII VIII	P	0	0	0	0	Yes
Tachinus fumipennis (Say)	H	VII	P	0	0	0	0	Yes
Tachinus memnonius Gravenhorst	P	IX	P	0	0	0	0	Yes
TENEBRIONIDAE								
Alleculinae								
Capnochroa fuliginosa (Melsheimer)	H	VI VII	F	0	0	2	2	Yes
Hymenorus obesus Casey	P	VI	FS	1	0	0	1	Yes
Hymenorus sp.	H	VII VIII	F	1	0	0	1	NA
Isomira oblongula Casey	CH	VI VIII IX	F	1	2	0	3	Yes
Isomira pulla (Melsheimer)	C	VII	F	0	1	0	1	Yes
Isomira quadristriata (Couper)	CO	VI VII VIII	FS	0	2	0	2	Yes
Isomira sericea (Say)	CHP	VII VIII IX	FS	1	2	1	4	Yes
Mycetochara bicolor (Couper)	HP	VI VII	F	1	0	1	2	Yes
Diaperinae								
Corticeus parallelus (Melsheimer)	HP	V VI VIII IX	F	4	0	0	4	Yes
Corticeus praetermissus (Fall)	H	V VI IX	F	7	0	0	7	Yes
Lagriinae								
***Anaedus brunneus* (Ziegler) ***	P	VI VII	P	0	0	0	0	Yes
Arthromacra aenea (Say)	GPS	VI VII	FS	1	0	0	1	Yes
Stenochiinae								
Strongylium tenuicolle (Say)	H	VI	F	0	0	1	1	Yes

TETRATOMIDAE								
Eustrophinae								
Eustrophus tomentosus Say	H	VII VIII IX	F	0	4	0	4	Yes
Synstrophus repandus (Horn)	H	VIII IX	F	0	4	0	4	Yes
THROSCIDAE								
Throscinae								
Aulonothroscus constrictor (Say)	H	VI VIII	F	1	2	0	3	Yes
***Aulonothroscus distans* Blanchard ***	P	V VI	F	1	0	1	2	Yes
Trixagus carinicollis (Schaeffer)	H	VIII	F	0	1	0	1	Yes
TROGOSSITIDAE								
Peltinae								
Thymalus marginicollis Chevrolat	CP	VI VII	F	2	0	0	2	Yes
Trogossitinae								
Airora cylindrica (Audinet-Serville)	CP	VI VII	F	2	0	0	2	Yes
ZOPHERIDAE								
Colydiinae								
Bitoma quadriguttata (Say)	P	V	F	0	0	1	1	Yes
Synchita fuliginosa Melsheimer	H	VI	F	0	1	0	1	Yes

[1] A species typed in bold and followed by the symbol * is considered a new state record for Michigan (N = 18), i.e., we are not aware of any published mention of it occurring in Michigan, either in print or online. A species name followed by ‡ (N = 14) indicates species for which Michigan specimens have been deposited in the Albert J. Cook Arthropod Research Collection (ARC) at Michigan State University (MSU) prior to our study and published on SCAN, but with no published records in print. Similarly, a species name followed by # (N = 1) indicates a species for which photographs of Michigan specimens have been posted on BugGuide, but with no specimens in the ARC-MSU collection, nor any published records in print. Species names not followed by a symbol (N = 336) already have a published in-print record of occurring in Michigan.
[2] Habitats: C = cedar, G = grassland, H = hardwoods, O = other but primarily the Rail Trail, P = pine, and S = Sedge Meadow Trail. See text for details.
[3] Months: V = May, VI = June, VII = July, VIII = August, and IX = September.
[4] Methods: F = funnel traps, P = pitfall traps, and S = sweeping.
[5] Funnel traps were baited with one of three lures: a-p = alpha-pinene, ETOH = ethanol, and Ips = ipsenol. See text for details. Numbers represent season-long totals of individuals collected by lure type and the total for all funnel traps combined. If no values are listed, then these species were not collected in the funnel traps.
[6] Species listed as "Yes" are considered native to the continental USA, and for those considered exotic to the USA, their native ranges are given as follows: Eur = European, EurAs = Eurasian, and Pal = Palearctic. NA = not applicable.
[7] Some sources have elevated certain subfamilies of Nemonychidae to family status, such as Cimberidinae being elevated to Cimberidae.

The Probability of Spotted Lanternfly, *Lycorma delicatula* (Hemiptera: Fulgoridae), Escape Differs Among Life Stages and Between Two Trapping Techniques Commonly Used by Landowners, Sticky Bands and Duct Tape

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Abstract

The invasive *Lycorma delicatula* (White) was first identified in Pennsylvania, U.S.A. in 2014, and has since increased its range to several Eastern states. *Lycorma delicatula* pose a serious threat to many native species, including hardwoods and grapes, and land owners are continually seeking effective traps to control populations. Both commercially-produced Web-Cote brand sticky bands and less expensive duct tape are often used by land owners to trap *L. delicatula*. However, the probability of escape from these adhesives has not been formally assessed, and almost certainly differs as a function of life stage and type of adhesive used. The purpose of this work was to determine if the effect of adhesive type (Web-Cote sticky bands vs. duct tape) on the probability of escape differs based on life stage. Additionally, we wanted to know how escape probability differs among life stages when individuals were exposed to each adhesive type, separately. In all life stages, the probability of escape from duct tape was greater than from Web-Cote sticky bands, indicating that sticky bands are a more effective tool in *L. delicatula* population control. In trials using only Web-Cote sticky bands, the probability of escape was low in second (21.1%), third (32.6%), and fourth (38.5%) instars relative to adults (84.1%). In trials using only duct tape, the probability of escape remained high among all life stages, with approximately 72% of second instars and 100% of adults escaping. Recent studies indicate that alternate trapping techniques, including circle trunk traps, are even more effective at capturing *L. delicatula* than sticky bands, though they are costlier. We propose a hybrid approach to *L. delicatula* trapping which utilizes relatively inexpensive sticky bands early in the season, and fewer, more effective circle trunk traps later in the season.

Keywords: sticky band, invasive species, *Ailanthus altissima*, pest management

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The spotted lanternfly, *Lycorma delicatula* (White), is an invasive planthopper native to China that was first detected in Berks County, PA, U.S.A., in 2014, and whose population sizes increased rapidly thereafter (Barringer et al. 2015, Dara et al. 2015, Parra et al. 2017). *Lycorma delicatula* has now been observed in thirty Pennsylvania counties, twenty-six of which are under quarantine due to infestations (Pennsylvania Department of Agriculture 2020, NYSIPM 2020). As of September 2019, the original 130 km^2 quarantine zone had increased to over 24,000 km^2 in Pennsylvania, Maryland, New Jersey, and Delaware, with an additional quarantine established in Frederick County, Virginia (Urban 2019, NYSIPM 2020). CLIMEX and MAXENT models suggest climate and habitat suitability is high for *L. delicatula* throughout many parts of the United States, as well as into South America (Jung et al. 2017, Wakie et al. 2020), and the spread and establishment of *L. delicatula* populations is expected to continue.

Lycorma delicatula's preferred host species is *Ailanthus altissima* (Mill.) Swingle (tree of heaven), an invasive that is common throughout the eastern United States (Dara et al. 2015). However, *L. delicatula* is not host-specific (as reviewed by Ding et al. 2006), and nymphs have been observed on a variety of species, including grapes, hops, cultivated trees, stone fruits, and native trees, including *Juglans nigra* L. (black walnut), *Asimina triloba* (L.) Dunal (pawpaw),

and *Acer sp* (maple), with a preference for *A. altissima* evident in late instars and adults (Lee et al. 2009, Park et al. 2009, Kim et al. 2011, Dara et al. 2015, Cooperband et al. 2018, Francese et al. 2020, N. Ritter 2000, personal communication). Both nymph and adult *L. delicatula* exhibit a cyclic behavior pattern wherein individuals climb upward on a vine or tree, fall or jump off often to avoid an obstacle or threat, and subsequently begin to re-ascend that or another host plant (Kim et al. 2011, Francese et al. 2020). Nymphs and adults feed on the leaves, stems, and branches of host plants by using piercing and sucking mouthparts to extract sugar-containing sap (as reviewed by Ding et al. 2006, Dara et al. 2015). Extensive feeding by large groups of *L. delicatula* can lead to open wounds, and the eventual wilting and death of tree branches (Dara et al. 2015). Additionally, the sticky honeydew excreted by *L. delicatula* during feeding coats lower vegetation and is readily colonized by sooty mold (as reviewed by Ding et al. 2006, Lee et al. 2009). *Lycorma delicatula* pose an ecological threat to forests throughout the eastern United States, and an economic threat to various industries including the production of grapes, hops, stone fruits, and cultivated tree stock (Lee et al. 2009, Dara et al. 2015, as reviewed by Lee et al. 2019). In an effort to prevent damage caused by *L. delicatula*, landowners are constantly in search of methods to eradicate individuals from their property.

Numerous trapping techniques have been tested in the field, including sticky bands, BugBarrier tree bands, circle trunk traps, and flight intercept traps (Francese et al. 2020). Francese et al. (2020) recommend the use of circle trunk traps, produced by modifying pecan weevil trunk traps (Great Lakes IPM, Vestaburg MI). Nevertheless, these commercially-available circle trunk traps are relatively expensive per unit, and may be financially inaccessible for private landowners. Many private landowners utilize cheaper, widely-available alternatives such as commercially-produced sticky bands and duct tape (Fig. 1).

Commercially-produced sticky bands are commonly used to control *L. delicatula*, yet the effectiveness is likely limited, as probability of capture undoubtedly varies based on life stage, with a disproportionate number of earlier instars being captured (Cooperband et al.2019, Francese et al. 2020). Indeed, field observations suggest that later instars and adults often crawl onto and back off of sticky bands with varying degrees of effort (Chandler, personal observation). However, the probability of *L. delicatula* escape from sticky bands has not been formally assessed, and information to this effect is valuable for informing banding protocol. Duct tape was initially suggested as a cheaper alternative to commercially-produced sticky bands, although experts warned that duct tape may be less effective because it loses its adhesive quality more quickly than sticky bands, especially after rain (Swackhamer 2018, Etters and Leach 2019). Indeed, duct tape is often observed wrapped around the trunks of trees in areas with large *L. delicatula* populations. Regardless, experimental trials have not tested the effectiveness of duct tape in capturing *L. delicatula*, and it is possible that many landowners are employing this technique with little-to-no success, especially when combatting late-instar nymphs and adults.

Studies have compared differences in the number of individuals captured using various trapping methods, but differences in catch may be confounded by the level of infestation in given areas and on given trees. Less is known about the probability of an individual escaping from a trap once the trap is encountered. After observing individuals of various life stages interacting with sticky bands in the field, we designed a controlled laboratory experiment to answer some simple, yet relatively unexplored questions: (1) Does the effect of adhesive type on the probability of escape vary based on life stage? We predicted that commercially-produced sticky bands would be more effective than duct tape in all life stages. (2) Does the probability of *L. delicatula* escape vary based on the insect's life stage, regardless of the type of adhesive band used? We predicted that the probability of escape across both adhesive band types would increase as life stage increased. (3) Does the probability of *L. delicatula* escape differ between commercially-produced sticky bands and duct tape, regardless of life stage? We hypothesized that even when brand new, duct tape will be inferior to sticky bands regardless of the insect's life stage. (4) For each of the two types of adhesive bands, separately, does the probability of escape vary among life stages? We predicted that the probability of escape from commercially-produced sticky bands will increase as individuals progress in life stage, but will remain relatively low, whereas the probability of escape from duct tape will remain high regardless of life stage. Tree banding is an easy tool for landowners to use in their fight against *L. delicatula*, however, it is probable that banding is not being done optimally, costing landowners valuable time and money. Our goal is to use novel data to answer the questions above, and to add to the growing knowledge base for best management practices in the control and management of *L. delicatula*.

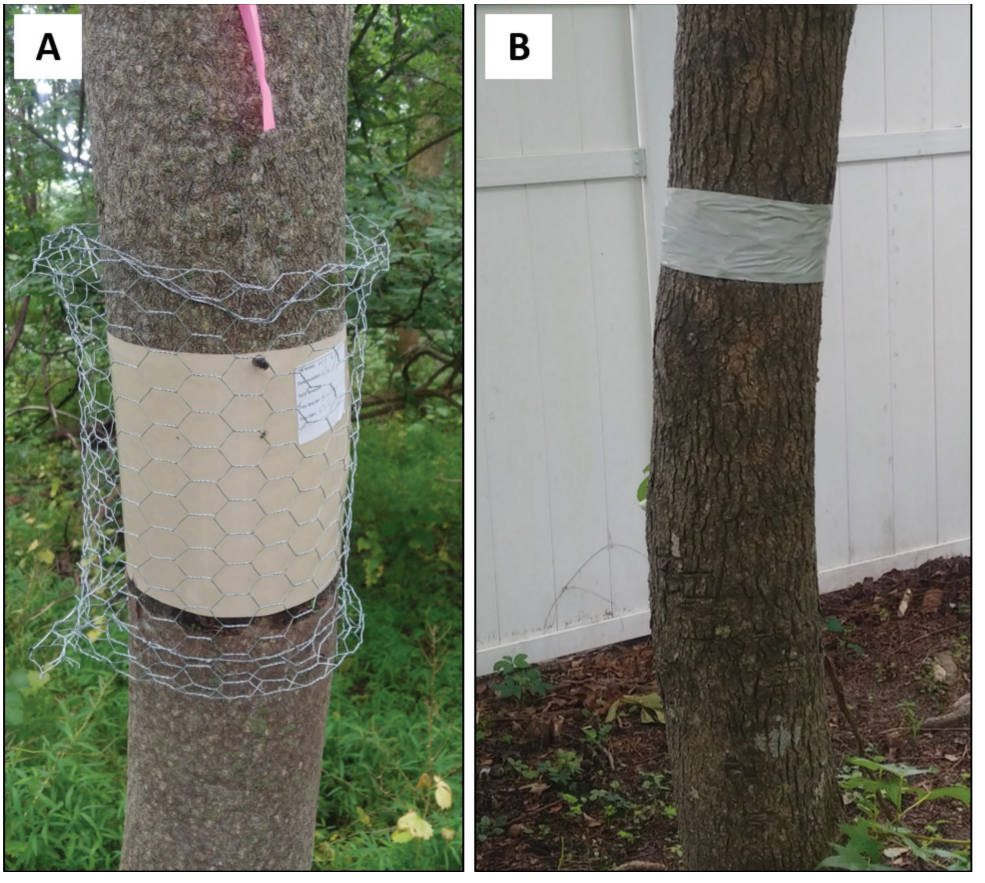

Figure 1. Trees equipped with (a) Web-Cote sticky band wrapped with wire mesh to prevent vertebrate bycatch, and (b) duct tape. Photo credit: Jennifer Chandler

Methods and Materials

In summer 2019, second (n = 41), third (n = 94), and fourth (n = 97) instar, as well as adult (n = 89) *L. delicatula* were captured from forest fragments throughout southeastern Pennsylvania. The opportunistic nature of this study precluded the capture of first instars. Individuals were carefully collected using mesh bags, and were immediately transported to the lab, which was located within the Pennsylvania *L. delicatula* quarantine zone, and held in a mesh enclosure containing fresh *A. altissima* branches for a period not exceeding 24 hours while they awaited testing.

The upper portion of a piece of wood (2.5 cmD × 10.2 cmW × 40.6 cmL), was wrapped completely in an approximately 7.2 cm tall strip of either Web-Cote brand sticky band (Web-Cote Industries, Hamburg, NJ) or Nashua professional grade duct tape (Berry Plastics Corporation, Franklin, MA). Fresh strips of adhesive material were utilized for each trial. Web-Cote sticky bands were utilized in this experiment because this brand was most effective in capturing both nymph and adult *L. delicatula* when compared to generic, clear packing tape and to brown adhesive bands produced by Korea Beneficial Insects Lab Co. (Cooperband et al. 2019). Professional Grade Nashua 398 All-Weather Heavy-Duty HVAC duct tape (11 mil) was used in this experiment, as this tape is an industrial-grade duct tape with a rubber-based adhesive, which forms stronger bonds than polymer-based adhesives. Additionally, the adhesive value (80 oz/in) of Nashua 398 as measured on steel (Berry Plastics Corporation 2011) surpasses the adhesive value of many standard, non-professional grade duct tapes commonly available and utilized by the public.

The adhesive-wrapped wood was oriented vertically within a separate mesh

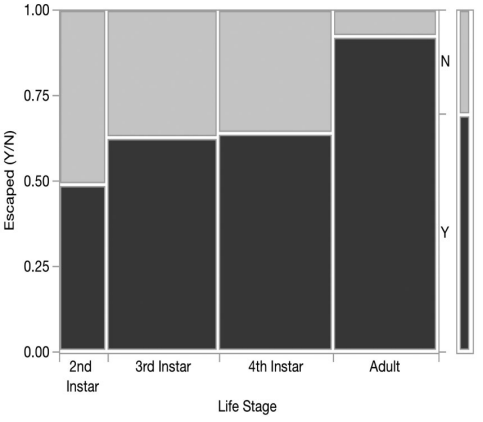

Figure 2. Proportion of individuals in each life stage escaping (dark gray) and being captured (light gray) when pooled across both adhesive band treatments ($\chi^2 = 36.495$, $P < 0.0001$, $n = 321$).

enclosure, the life stage of a single, randomly-selected *L. delicatula* was recorded, and that individual was carefully released near the base of the piece of wood and allowed to climb vertically to the trap. When necessary, individuals were encouraged to climb upward toward the trap by orienting a small object several inches below the individual, and allowing them to move upward toward the trap and away from the introduced object. Once the individual encountered the adhesive and an escape attempt was initiated, a timer was set for two minutes, within which time the individual could attempt to escape. The two-minute duration was established as the escape threshold based on preliminary observations that lasted for time periods greatly exceeding two minutes. These observations indicated that if the *L. delicatula* failed to escape after two minutes, it was unsuccessful in ever freeing itself. The ability or inability of an individual to escape within the allotted time was recorded. The same process was repeated for each individual collected (n = 321).

Log-likelihood analyses were used to test our hypotheses, with escape (Yes or No) as the nominal response variable, and adhesive type (levels: sticky band and duct tape) and life stage (levels: 2–4 instar and adult) as nominal explanatory variables. A 2 × 4 factorial log-likelihood was performed to evaluate if there is a differential effect of adhesive type and life stage on escape probability (question 1, above), if escape probability varies among life stages, across both adhesive types (main effect 1—question 2, above), and if escape probability differs between adhesive type, averaged across all life stages (main effect 2—question 3, above). To determine how the effectiveness of each band type differs as *L. delicatula* progress to later instars and eventual adults (question 4, above), we split the observations into two groups based on the type of adhesive band used, and we evaluated whether the probability of escape from that band type varies among life stages using log-likelihood. All analyses were performed using JMP Statistical Discovery software (JMP 2019)

Table 1. Percentage of *L. delicatula* that escaped from each type of adhesive band within each life stage.

Life Stage	% Escaped (Sticky Band)	% Escaped (Duct Tape)
2nd Instar	21.1	72.7
3rd Instar	32.6	91.7
4th Instar	38.5	93.3
Adult	84.1	100

Results

The effect of life stage on escape probability did not depend on the type of adhesive band used (Likelihood Ratio $\chi^2 = 1.7149$, $P = 0.6336$). For each life stage, the proportion of individuals escaping was substantially greater when using duct tape than when using sticky bands (Table 1).

The probability of an individual escaping differed depending on life stage (Fig. 2; Likelihood Ratio $\chi^2 = 36.495$, $P < 0.0001$). The percentage of *L. delicatula* able to escape was lowest in 2nd instars (48.8%), was similar among 3rd (62.8%) and 4th (63.9%) instars, and was greatest among adults (92.1%), when pooled over both band types (Fig. 2). The type of adhesive band used influenced the probability of *L. delicatula* escape (Likelihood Ratio $\chi^2 = 70.544$, $P < 0.0001$), with only 47.2% of individuals ranging from 2nd instar to adults escaping from the sticky bands, and 91.9% escaping from duct tape, (Fig. 3).

To better understand the effectiveness of each of the separate adhesive bands in capturing different life stages, we performed analyses which focused solely on individuals introduced to each of the two band types. The first analysis, which focused only on individuals subjected to sticky band trials, indicated that life stage influences the probability of escaping from sticky bands (Likelihood Ratio $\chi^2 = 37.196$, $P < 0.0001$). The proportion of individuals that escaped from sticky bands increased with life stage progression, with a marked increase in escape observed in adult *L. delicatula* (Fig. 4). A separate analysis which focused only on individuals exposed

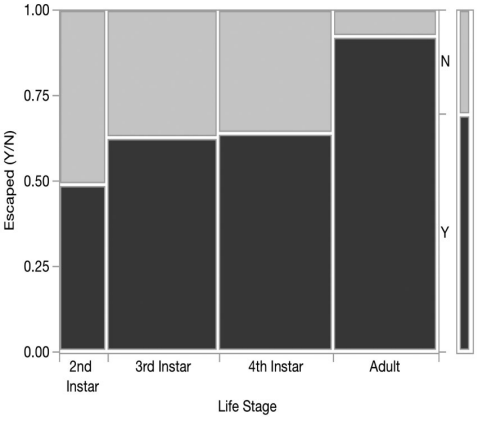

Figure 3. Proportion of individuals escaping (dark gray) and being captured (light gray) on sticky bands (n=161) and duct tape (n= 160) when pooled across all life stages (χ^2 = 70.544, P < 0.0001).

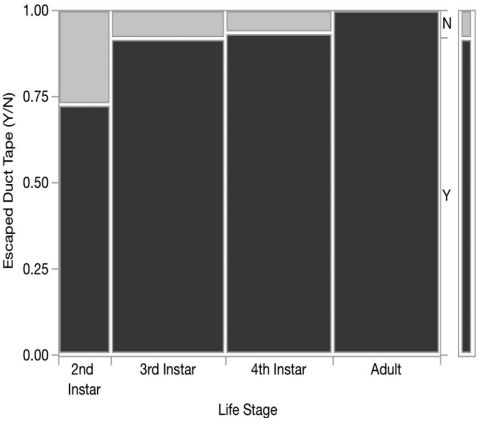

Figure 5. Proportion of individuals in each life stage escaping from duct tape (dark gray) and being captured by duct tape (light gray) (χ^2 = 14.818, P = 0.0020, n = 160).

to duct tape trials also indicated that life stage influences the probability of escaping duct tape (Likelihood Ratio χ^2 = 14.818, P = 0.0020). One-hundred percent of adults escaped from duct tape, and while the probability of escape was somewhat lower in 2nd instars (72.7%), the proportion of individuals that escaped was still high among all life stages (Fig. 5).

Discussion

Sticky bands are a popular, recommended method for reducing populations of the invasive *L. delicatula*. Alternatively, duct tape is suggested as a cheaper, readily available option for private use (Etters and Leach 2019). We tested the effectiveness of both methods to determine which led to a higher probability of *L. delicatula* capture throughout nymphal and adult life stages. The likelihood of *L. delicatula* escape was highest in more advanced life stages regardless of band type, though Web-Cote sticky bands were more effective than duct tape overall. Additionally, duct tape appears wholly ineffective in capturing adult *L. delicatula* (0% captured) whereas sticky bands were somewhat more effective in capturing adults (15.9% captured). Generally, these results suggest that placing Web-Cote sticky bands out when *L. delicatula* are still in early nymphal stages, as opposed to adults, will result in greater capture of early instar *L. delicatula*, will facilitate population reductions, and will consequently reduce the number of individuals that will become breeding adults.

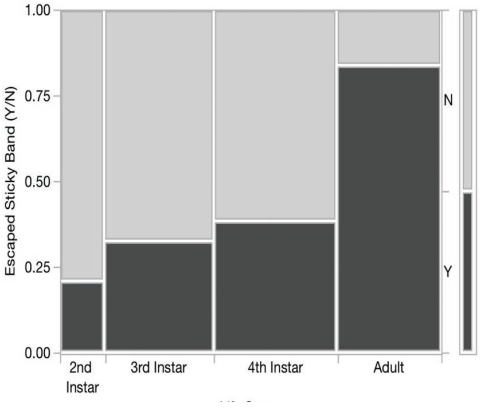

Figure 4. Proportion of individuals in each life stage escaping from sticky bands (dark gray) and being captured by sticky bands (light gray) (χ^2 = 37.196, P < 0.0001, n = 161).

First instars were not utilized due to the opportunistic nature of this experiment. However, based on the results of this experiment we expect that 1st instars would have the lowest probability of escape on both adhesive types. Anecdotal evidence suggests that some proportion of 1st instars are captured by duct tape, but the actual probability of capture is uncertain. As such, it is possible that landowners may have some degree of success capturing 1st instar *L. delicatula* using duct tape if the tape is placed out early to align with the beginning of the *L. delicatula* life cycle, and is replaced often. Additionally, landowners may choose to wrap trees with multiple bands of duct tape to increase the width of the surface on which early instars

Figure 6. An adult spotted lanternfly (*Lycorma delicatula*) avoids being captured on the adhesive by utilizing the wire mesh that has been placed around a sticky band to prevent vertebrate bycatch. Photo credit: Jennifer Chandler

may be captured. Nevertheless, duct tape appears far less effective than Web-Cote sticky bands, and landowners that use duct tape to capture 1st instars will need to switch to alternate methods to effectively capture individuals that are advanced beyond the 1st instar life stage. Only one brand of duct tape was used in this experiment, and as such, we must avoid making sweeping generalizations about the effectiveness of *all* types and brands of duct tape. Even so, the brand chosen was professional grade and had high adhesive value, and while other brands may vary slightly in effectiveness against *L. delicatula*, it is unlikely that the overall results would be significantly altered.

Results obtained from this study were from a controlled laboratory setting, and as such, they may represent "best case scenario" capture rates. Field conditions, including temperature variations, precipitation, and the accumulation of debris on the adhesive surface between band changes, can influence capture rate. Etters and Leach (2019) suggest that duct tape loses much of its adhesive quality when wet, and field observations indicate that the same is true of commercially-produced sticky bands (Chandler, personal observation). Additionally, if a significant amount of debris (leaves, twigs, dead carcasses of captured insects, etc.) accumulates on the adhesive between band changes, *L. delicatula* can use the debris as a "bridge" over the adhesive (Chandler, personal observation). Further, it is highly recommended that wire mesh, such as chicken wire, be placed around sticky bands to prevent bycatch of birds and small mammals (Finlay and Seifrit 2018, Etters and Leach 2019). We often observed *L. delicatula* crawling up the wire mesh that was situated at

least 1-inch away from the main stem with only the top and bottom of the mesh in contact with the tree, thus avoiding the adhesive (Fig. 6; Chandler, personal observation). As such, the probabilities of capture reported in this laboratory study are likely higher than can be expected when bands are placed in field conditions.

Recently, both the effectiveness of sticky bands modified with attractant lures as well as the effectiveness of alternate trapping methods have been assessed (Cooperband et al. 2019, Francese et al. 2020). Cooperband et al. (2019) tested for attraction of *L. delicatula* to several volatile compounds and found that methyl salicylate (wintergreen oil) attracted all life stages, and further determined that sticky bands baited with methyl salicylate resulted in up to a four-fold increase in capture when compared to sticky bands that lacked the volatile lure. A separate study compared the number of *L. delicatula* captured among several types of physical traps, including Web-Cote sticky bands, BugBarrier Tree Bands (Environmetrics Systems USA, Inc., Victor, NY), and circle trunk traps (modified pecan weevil traps, Great Lakes IPM, Vestaburg, MI), among others (Francese et al. 2020). Francese et al. (2020) did not assess the probability of escape once the trap was encountered, as did the current study, but rather investigated the mean number of individuals captured on trees that are equipped with different types of traps. Francese et al. (2020) compared standard Web-Cote sticky bands and BugBarrier bands, a trap design in which the adhesive surface faces inward toward the tree with a gap between the band and tree that provides access to climbing insects. Their results indicated that the number of early stage *L. delicatula* captured did not differ among the two traps, but that BugBarrier bands trapped more late-instar and adult individuals (Francese et al. 2020). Further, while there was no difference in the number of early stage *L. delicatula* between BugBarrier bands and circle trunk traps, circle trunk traps captured more 4th instars and adults (Francese et al. 2020).

When deciding which trapping method to use, landowners must consider the quantity of trees on which they need to place traps as well as the monetary and time investments that go into each type of trap. It seems that Web-Cote sticky bands wrapped with wire mesh to avoid bycatch are still a viable option in efforts to reduce population sizes. However, perhaps there is a more thoughtful, hybrid approach wherein relatively cheap, easy to use Web-Cote sticky bands baited with methyl salicylate are deployed on a diverse array of species early in the season to effectively capture generalist, early-stage nymphs. Then, as host preference trends toward *A. altissima* later in the season (Kim et al. 2011), landowners may target fewer trees with the costlier traps that are more effective against late-instars and adults, also baited with methyl salicylate. This hybrid approach, or perhaps a similar approach, may be time- and cost-effective for private landowners. Additionally, this approach will maintain expected capture rates over the season, while also substantially reducing the occurrence of problems associated with traditional sticky bands, such as vertebrate bycatch, by simply reducing the amount of time that traditional sticky bands are deployed.

Acknowledgments

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Sirex nigricornis (Hymenoptera: Siricidae) Larval Development Correlated with Tree Characteristics and Ophiostomoid Fungal Infection

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Abstract

The native North American woodwasp, *Sirex nigricornis* F. (Hymenoptera: Siricidae), has received significant attention over the last several years due to the introduction and successful establishment of the European woodwasp, *S. noctilio* F. in eastern North America. Larval size and development of *S. nigricornis* are important variables that can help to compare demography of the two species and predict future interactions. We measured head capsule width, body length, and weight of *S. nigricornis* larvae removed from 14 pine trees, felled across the Ozark and Ouachita National Forests of Arkansas in 2012. We also recorded the height at which larvae were removed, and the diameter of the stem at that height. We used logistic regression to compare proportions of larvae removed from each section of each tree. Two-thirds of the larvae collected came from a single tree. Most larvae were in the lower and middle sections of trees and larval size was positively correlated with tree diameter. Ophiostomatoid fungi were absent in trees that produced the highest number of larvae, implying *S. nigricornis* colonized those trees before bark beetles. These results have implications for interspecific competition and interactions among *S. nigricornis* and *S. noctilio,* and for management which relies on successful larval development to transmit parasitic nematodes.

Keywords: *Sirex*, *Ophiostoma,* invasive species

Over the last several years, *Sirex nigricornis* F. (Hymenoptera: Siricidae) has received significant attention due to the North American introduction and establishment of *S. noctilio* F., a globally invasive pest (e.g. Hajek et al. 2013, Chase et al. 2014, Hartshorn et al. 2016b). The interactions among *S. noctilio, S. nigricornis*, and other pine-inhabiting insects, as well as their associated fungi, are important from an ecological standpoint; fewer native woodwasps and associates are found in trees infested by *S. noctilio* (Ryan et al. 2012). Their interactions are also important from a management stand point. A parasitic nematode native to North America, *Deladenus proximus* Bedding, has been able to colonize *S. noctilio* as a host and infect its eggs and mycangia (Yu et al. 2011, Morris et al. 2013). Fungal competition among the *Sirex* symbiont, *Amylostereum* Boidin (Russulales: Amylostereaceae), and bark beetle transmitted *Ophiostoma* Syd. & P. Syd., as well as tree defenses, have been implicated in *S. nigricornis* and *S. nocilio* egg and larval mortality (Haavik et al. 2015). While *A. areolatum* (Chaillet ex. Fr.) Boidin is associated with *S. noctilio* and *A. chaillettii* (Pers.) Boidin is associated with *S. nigricornis*, both woodwasp species are able to use both fungal species in development (Hajek et al. 2013). Both fungal species are easily outcompeted by bark beetle-associated ophiostomoid fungi which is likely due to the rapid decline in tree moisture content following infection (Ryan et al. 2011, Hubbard et al. 2013).

Understanding *Sirex* larval development is important in predicting how these species may interact in the future, relating to spread of *S. noctilio* into the "wood basket" of the southeastern United States. Spatial niche partitioning (e.g. Paine et al. 1981) is common among wood-boring insects as is significant size variation which is likely due to low mobility of wood-boring larvae, as well as host nutritional quality (Andersen and Nilssen 1983). Comparisons among size variation and larval development of *S. nigiricornis* and *S. noctilio* may assist in making management decisions in areas where the two species will overlap.

Both *Sirex* and associated parasites, namely *Deladenus* nematodes (Tylenchida: Neotylenchidae), utilize a symbiotic fungus,

Amylostereum for development within the tree (Madden 1981, Yu et al. 2011). The nematode feeds directly on the fungus while free-living in the tree. *Sirex* larvae utilize specialized mandibles and N-fixing gut bacteria to extract nutrients and sugars from partially-degraded wood just behind the *Amylostereum* growth front (Thompson et al. 2014). Both *S. nigricornis* and *S. noctilio*, as well as multiple species of *Deladenus*, are able to develop on different species of *Amylostereum* (Hajek et al. 2013). Their reliance for development on a symbiotic fungus suggests that competition with other tree-inhabiting fungi, like *Ophiostoma*, may negatively affect both the woodwasp and its associated parasites (Yousuf et al. 2014, Yousuf et al. 2018). Species of *Ophiostoma* are commonly encountered fungi in pines in the United States that cause "bluestain" and are vectored by bark beetles (Coyle et al. 2016). Competition between these two fungal groups is likely affected by which insect species arrives at the tree first and this likely affects larval development, adult emergence, and therefore, future populations.

Our objective was to quantify the effects of tree height, diameter, and infection by ophiostomatoid fungi on larval development by examining number and size of larvae along the length of whole trees that were felled and left in the field for a year. We predict that, due to niche partitioning and intraspecific competition, more larvae will be present in the lower section of the tree where a larger diameter may support more larval development. We also predict that colonization by ophiostomatoid fungi will result in fewer developing larvae due to competition with *Amylostereum*.

Materials and Methods

In August 2010, eight loblolly pine (*Pinus taeda* L.) and six shortleaf (*Pinus echinata* Mill.) trees were felled in the Ozark and Ouachita National Forests in Arkansas and held in the field until July 2011 at which time they were returned to the lab, cut into 95 1-m long bolts (logs) up to a diameter of 12.7 cm, and split into slabs (slices) using a band saw and hatchet. Wood slabs were then dissected using a chisel. All larvae found during dissections were collected and head capsules (mm) and body length (cm) measured using calipers. Diameter (cm) was measured for each bolt, and height position along the bole was recorded as low (L), middle (M) or high (H) by dividing the total length of each tree into thirds. Presence of ophiostomatoid fungi (0 = absent, 1 = present) was also recorded for each bolt by visual confirmation of staining.

To determine effects of ophiostomatoid fungi on larval development, multiple regression was used with presence of fungi as the independent variable and total number of larvae as well as proportion of larvae per bole height (L, M, H) as dependent variables. To establish whether height along the bole (L, M, H) affected larval survival, a binomial regression with a logit link function (Whitlock and Schluter 2015) was created with height as the independent variable and proportion of larvae in each section as the dependent variable. Proportion of larvae was calculated by dividing the number of larvae from each section by the total number of larvae per tree. To quantify the effects of bole diameter on larval size, a Pearson's product-moment correlation test was used to calculate the correlation coefficient between body length and head capsule (0.68). Because the two size factors were significantly correlated (t = 12.948, $P < 0.0001$), a single linear model was created with log head capsule width as the response variable and diameter as the independent variable. All analyses were performed in RStudio (RStudio Team 2020).

Results

A total of 201 larvae across 14 trees was collected. All larvae were late instars, and appeared to be of a single cohort. Of the 14 trees that were felled, eight contained bolts with ophiostomatoid fungi. In trees with the fungus, it was present throughout nearly the entire bole. *Ophiostoma* did not significantly affect the proportion of *S. nigricornis* larvae in each section (F = 0.006, P = 0.936) but it did significantly affect the total number of larvae collected (F = 7.122, P = 0.0109). The vast majority of *S. nigricornis* larvae (168; 84%) were collected from trees that did not contain ophiostomatoid fungi.

Of the 201 total larvae, 133 (66%) were removed from a single tree collected from the Ouachita National Forest. Significantly more *S. nigricornis* larvae were found in the lower and middle sections of the trees (F = 6.013, P = 0.0053; Table 1) and head capsule width of *S. nigricornis* larvae was significantly positively affected by tree diameter (F = 8.858, P = 0.0033; Fig. 1).

Discussion

Our prediction of more larvae in the lower section of the tree was validated. However, a third of all *S. nigricornis* larvae collected were from a single tree, which makes extrapolation across trees difficult. These results do, however, fit with previous studies showing *S. noctilio* attack distribution to be highly aggregated in a few trees within stands (Lantschner and Corley 2015). While *S. nigricornis* attacks do not produce

Table 1. Characteristics of trees collected for dissection.

Tree #	Location	# Bolts	Total Height (m)	DBH (cm)	Species	# *Sirex* larvae	*Ophiostoma* (%)
1	Ouachita NF	6	6	30.5	Loblolly	2	0
2	Ouachita NF	8	8	35.5	Loblolly	133	0
4	Ouachita NF	7	7	16	Loblolly	2	100
64	Ouachita NF	5	8.8	21.2	Loblolly	2	50
66	Ozark NF	5	5.25	45.2	Shortleaf	1	100
67	Ozark NF	5	5.25	26.7	Shortleaf	3	100
68	Ouachita NF	8	11.9	28.5	Loblolly	4	100
69	Ouachita NF	10	14.6	34.3	Loblolly	15	100
71	Ouachita NF	7	11	27.9	Shortleaf	3	33
72	Ozark NF	5	5.25	26.3	Shortleaf	3	100
74	Ozark NF	7	9.5	25.4	Shortleaf	2	0
75	Ozark NF	5	8	28.5	Shortleaf	2	0
76	Ouachita NF	5	8.8	26.7	Loblolly	6	0
77	Ouachita NF	12	16.2	31.2	Loblolly	23	0

resinosis as do *S. noctilio* attacks (Ryan et al. 2013), previous studies have found that females strongly prefer fresh trees but development is highest in trees with moderate moisture loss (Hartshorn et al. 2016a). Individual trees serving as the main reservoir for developing *Sirex* larvae implicates between-tree variation in variables such as moisture and tree defenses, as a major driver of larval development and survival. This has been found for *S. noctilio* natural and lab-reared cohorts (Haavik et al. 2016). Based on previous studies looking at *S. nigricornis* oviposition preferences related moisture loss in pines (Hartshorn et al. 2016a), the aggregation found in this study suggests that the trees with the highest number of larvae were those with moderate moisture stress, likely related to ophiostomoid fungal infection associated with bark beetle infestation (Hubbard et al. 2013).

Ophiostomatoid fungi were found in eight of the 14 total trees, and across nearly the entire bole of those eight trees (Table 1). Research has investigated interactions among *Sirex* and wood-boring beetles, with fungal competition appearing to play a major role (Hurley et al. 2012). Competition among *Amylostereum* and *Ophiostoma* has implications for larval development (Thompson et al. 2014) as well as management in that the parasitic nematode used in biological

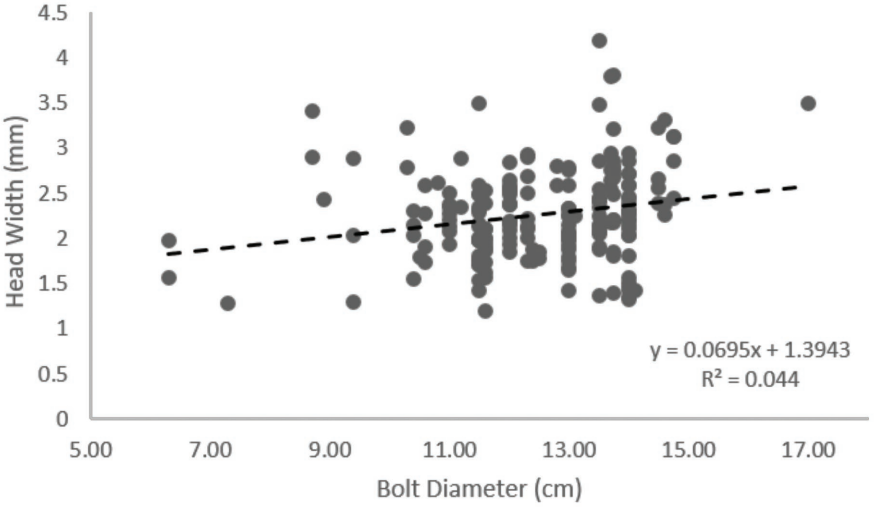

Figure 1. Linear model of larval head capsule width across bolt diameter with equation and R^2 reported.

control of *S. noctilio, Deladenus siricidicola* Bedding, feeds on *Amylostereum*. Due to this reliance on *Amylostereum,* the development of both the woodwasp and nematode may be hindered in the presence of ophiostomatoid fungi (Yousuf et al. 2018). Because our trees were left in the field for nearly a year, all larvae collected were late-instar and represent a final natural cohort. Based on fungal competition studies, we can infer that *S. nigricornis* was the first insect to arrive at trees with the most successful larval development. On the trees infected with ophiostomatoid fungi, bark and ambrosia beetles likely arrived prior to *S. nigricornis*.

Significantly more larvae were found in the lower and middle sections of the tree compared to the top sections. This contrasts with studies that have found consistent emergence along the length of the bole with no effect of height, although more, and larger, *S. noctilio* were found in larger trees (Ryan et al. 2012). In our study, larvae were significantly larger in the lower sections of the tree. Most mortality of *S. noctilio* occurs during the egg and neonate stage (Haavik et al. 2015) and we assume this to be true for *S. nigricornis* as well. Host preference tests have shown that *S. noctilio* prefers the European species, Scots pine (*P. sylvestris* L.) but will drill into, and emerge from, North American pines such as red pine (*P. resinosa* Aiton) Virginia pine (*P. virginiana* Mill.) and eastern white pine (*P. strobus* L.) (Dinkins 2011). However, no adults emerged from Loblolly pine (*P. taeda*) in their study.

Our results suggest that larval survival is highest in the middle section of trees without ophiostomatoid fungal infection which also suggests that survival is highest in trees where *S. nigricornis* is the first insect to colonize the tree. These results support studies on *S. noctilio* and imply that interspecific competition will minimize spread of *S. noctilio* into the southeastern United States. Interspecific competition is likely among these groups as it is most common in sessile, aggregated, introduced insects (Denno et al. 1995). Demography and within-tree interactions among the two species, as well as other wood borers, warrant investigation to elucidate potential future impacts of *S. noctilio* spread.

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First Report of *Enoclerus spinolae* (LeConte) (Coleoptera: Cleridae) from Missouri and Nebraska

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Abstract

New state records are presented for *Enoclerus spinolae* (LeConte) (Coleoptera: Cleridae) specimens from Missouri and Nebraska.

Key words: *Enoclerus spinolae*, Coleoptera, Cleridae, state records, Missouri, Nebraska

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The checkered beetle *Enoclerus spinolae* (LeConte) (Coleoptera: Cleridae) is reported from Missouri for the first time with five individuals collected at Star School Hill Prairie Natural Area (south unit). This preserve is a Loess Hills prairie remnant overlooking the Missouri River Valley north of the town of Rock Port (Atchinson County) and is located about two miles (3 km) south of the state border with Iowa. All specimens were collected 30 June 2016 on flowering yucca plants. Four of the specimens were collected by Marlin E. Rice (pers. comm., July 2016). The fifth specimen was collected by M. J. Hatfield who posted a photo online at http://bugguide.net/node/view/1250952 (pers. comm., July 2016).

The first state record for *E. spinolae* for Nebraska was posted on the internet by Johan Pretorius: http://bugguide.net/node/view/865393 [copyright 2013 Elytron] (pers. comm., July 2016). This beetle specimen was collected at Scottsbluff, Scotts Bluff Co., Nebraska, 20 July 2013. Subsequently several more Nebraska specimens were located in the University of Nebraska State Museum insect collection, Lincoln (UNSM) and in the personal collection of M. J. Paulsen (MJPC) (pers. comm., July, September 2016). Specimen label data include records for seven Nebraska counties [numbers of specimens in brackets]: Thedford, Thomas Co., Nebraska, August 1953 [1] (UNSM); Wauneta, Chase Co., Nebraska, 15 July 1954 [1] (UNSM); Valentine National Wildlife Refuge, Cherry Co., Nebraska, June 1968 [3] (UNSM); Sandhills Ag Lab, McPherson Co., Nebraska, 8–14 July 1973 [3] (UNSM); Halsey National Forest, Nebraska, July 1969 [9], July 1984 [1] (UNSM), 28 September 2011 [1] (MJPC); Arapaho Prairie, Arthur Co., Nebraska, 29 July 1984 [2], 11 August 1984 [3], 22 July 1985 [3], 17 July 1986 [6], 28 July 1987 [2], August 1987 [1], 29 July 1988 [8] (UNSM), 12 June 2000 [1] (MJPC); Lake McConaughy, Keith Co., Nebraska, 18 June 2000 [1] (MJPC); Sanborn, Dundy Co., Nebraska, 27 June 2004 [1] (MJPC); Merrittt Reservoir, Cherry Co., Nebraska, 2 August 2016 [1] (MJPC).

John L. LeConte (1853) originally described this beetle species as *Clerus spinolae* from specimens collected near the Mexican border by John Henry Clark of the U. S. Corps of Topographical Engineers led by Col. James Duncan Graham (Geiser 1936). The species name honors entomologist Maximilian Spinola author of the first world monograph on clerids (LeConte 1853). Charles J. Gahan (1910) transferred all North American species of the genus *Clerus* Geoffrey, 1762 to the New World genus *Enoclerus* Gahan, 1910. Albert B. Wolcott (1947) later synonymized this species name under *Enoclerus abdominalis* (Chevrolat, 1835). Barr (1976) declared this name to be an invalid junior homonym and replaced it with *Enoclerus zonatus* (Klug, 1842) with *E. spinolae* as its junior synonym. Barr and Rifkind (2009) resurrected *Enoclerus spinolae* (LeConte, 1853) to a full species after examining many specimens from many locations (Rifkind, pers. comm., July 2016). This southwestern checkered beetle has been previously reported from Arizona, California, Colorado, Kansas, Nevada, New Mexico, Texas, Utah, and Mexico (Leng 1920, Wolcott 1947, Barr and Rifkind 2009). *Enoclerus spinolae*, a predaceous beetle species, is frequently found among the blossoms of yuccas (Agavoideae) (Wickham and Wolcott 1912, Boving and Champlain 1921, Davis 1967, Foster and Barr 1972).

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Bark- and Wood-Infesting Coleoptera and Associated Parasitoids Reared from Shagbark Hickory (*Carya ovata*) and Slippery Elm (*Ulmus rubra*) in Ingham County, Michigan

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Abstract

Ten species of bark- and wood-infesting Coleoptera (borers) and five parasitoid species (Hymenoptera) were reared from shagbark hickory [*Carya ovata* (Mill.) K. Koch] branches 1-2 years after tree death, and similarly, seven borers and eight parasitoids were reared from slippery elm (*Ulmus rubra* Muhl.) branches one year after tree death in Ingham County, Michigan, in 1986-87. The borers were species of bostrichids, buprestids, cerambycids, and curculionids (including Scolytinae). The parasitoids were braconids, chalcidids, eurytomids, ichneumonids, and pteromalids. One new larval host record was recorded: the cerambycid *Urgleptes querci* (Fitch), being reared from *U. rubra*. This paper presents new Michigan state records for the eurytomids *Eurytoma conica* Provancher and *Eurytoma phloeotribi* Ashmead, the ichneumonid *Xorides humeralis* (Say), and pteromalid *Cheiropachus quadrum* (Fabricius). At the same field site where the above rearings occurred, when newly cut shagbark hickory branches were placed on the ground and at two canopy levels in a healthy hickory tree in May 1986 and then collected 11 months later in April 1987 and placed in rearing cages, borers (two species) and parasitoids (four species) were reared from the branches that had been suspended in the canopy, but none emerged from the branches that had been on the ground, suggesting vertical stratification of both borers and parasitoids.

Keywords: Borers, parasitoids, Hymentoptera, phoretic mites, host range, state records

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During my working career with the Northern Research Station of the U.S. Forest Service (1986-2015), which has had a Forest Insect Research Unit on the Michigan State University campus since 1956 (Haack 2006), I lived on a 13 ac (5.3 ha) rural property near Dansville, Ingham County, MI (N 42.5481° Lat, W 84.3189° Long). Over 80% of that property was covered by mature northern hardwood (beech-maple) forest. When combined with the neighboring properties, the contiguous woodlots covered over 60 ac (24 ha). The dominant tree species were sugar maple (*Acer saccharum* Marshall) and American beech (*Fagus grandifolia* Ehrh.), followed by yellow birch (*Betula alleghaniensis* Britton), bitternut hickory [*Carya cordiformis* (Wangenh.) K.Koch], shagbark hickory [*Carya ovata* (Mill.) K. Koch], white ash (*Fraxinus americana* L.), black cherry (*Prunus serotina* Ehrh.), northern red oak (*Quercus rubra* L.), white oak (*Quercus alba* L.), American basswood (*Tilia americana* L.), and slippery elm (*Ulmus rubra* Muhl.). Also present, but less common, were tree species in the genera *Amelanchier*, *Carpinus*, *Ostrya, Populus, Prunus,* and *Zanthoxylum*. On several occasions at this Dansville location, I reared bark- and wood-infesting insects and their associates from branch and trunk sections of various tree species. My earliest rearing records were from *C. ovata* and *U. rubra* in 1986-87, and that is the focus of this paper. Although these findings are many years old they are still valuable given that they document larval host records, adult emergence periods, and at times new state records for Michigan insects.

Some of the first major publications to summarize the life cycles of common North American bark-and wood-infesting insects (borers) were by Packard (1890) and Felt (1905). Many similar books have followed, with the most recent book focusing on North American borers that infest hardwood trees (Solomon 1995). Early studies on borers associated with hickory (*Carya* spp.) often focused on the hickory bark beetle, *Scolytus quadrispinosus* Say (Coleoptera: Curculionidae: Scolytinae), which has often reached outbreak levels in the eastern United States (Hopkins 1912, Blackman and Stage 1924, Solomon 1995). By contrast, early studies of borers infesting elm (*Ulmus* spp.) usually focused on the elm borer, *Saperda tridentata*

Olivier (Coleoptera: Cerambycidae) (Packard 1890, Felt and Joutel 1904). Later, in the early decades of the 1900s, after the introduction into the eastern United Sates of the smaller European elm bark beetle [*Scolytus multistriatus* (Marsham) (Coleoptera: Curculionidae: Scolytinae)], and the *Ophiostoma* fungal pathogens that cause Dutch elm disease, several studies were conducted on the major borers and other insects associated with elm that could possibly transmit the fungal spores (Hoffman 1939, Hoffman 1942, Pechuman 1940).

Methods. Study 1. On 19 April 1986, I cut down four *C. ovata* and *U. rubra* trees that had died in the Dansville woodlot in summer 1985 and had remained standing. While cutting the trees, I noticed they were infested with borers (bark- and wood-infesting insects), and therefore decided to place some of the host material in rearing cages. I soon obtained six rearing cages (ca. 60 cm wide, 45 cm deep, and 45 cm tall) that each had a wood floor, a sliding Plexiglas front panel, and fine screening on the other three side walls and upper surface. The cages were placed on a counter, inside a covered shed (ca. 8 × 12 ft or 2.4 × 3.7 m), that had double doors at opposite ends that remained open to allow good air flow. The shed received direct sunlight during the early morning hours, but otherwise was shaded and therefore the temperatures inside the shed were similar to ambient conditions.

On 3 May 1986, I collected two *C. ovata* and three *U. rubra* branches that had been left on the forest floor when I cut the standing trees on 19 April. I selected branches that had evidence of borer attack, such as larval galleries being evident at the cut ends of the branches where they had been attached to the trunk. The branches were 8–10 cm in diameter at their base. The branches were cut in sections to fit inside the rearing cages and utilized down to a branch diameter of about 2 cm. The total length of all branch sections, if placed end to end, was about 12 m for *C. ovata* and 16 m for *U. rubra*. In addition, about 400 cm^2 of the outer bark was removed from the upper trunk of one *U. rubra* tree that had been cut on 19 April, where the diameter was about 20–25 cm diameter. The branch and bark samples were placed separately by tree species inside the rearing cages, and usually checked every 1-2 days for recently emerged insects through August 1986, and then less frequently through October 1986. The elm branches were discarded in November 1986. However, the hickory branch sections were kept in the same cages, outdoors, through the winter, and then checked every 1–2 days for newly emerged insects from mid-April through May 1987. After each collection, all insects were placed in labeled vials by tree species and date and then frozen. Later, once individuals of each morphospecies had been identified, often by experts (see acknowledgments), the insects were totaled by species and emergence date. Specimens of each species were retained by the identifiers in their personal or institutional collections. All parasitoids were identified by staff at the US Department of Agriculture, Systematic Entomology Laboratory in Beltsville, MD.

Study 2. A second study was conducted in 1986–87 to explore how borer and parasitoid infestation levels varied with canopy height. On 28 May 1986, I cut 12 branches from a single, small, healthy *C. ovata* tree in the Dansville woodlot. The branches appeared uninfested at the time of cutting, and they measured 1.2–2.0 m long and 2–6 cm in diameter at their widest end. Four branches, representing a range of sizes, were placed at three heights in another nearby *C. ovata* tree on 28 May 1986. The selected hickory tree was about 10 m tall and grew near the edge of the woodlot (within 10 m). Four of the cut branches were placed on the ground around the base of this tree (ground level), four branches were suspended from lower-canopy branches (ca. 3 m aboveground; lower canopy), and four branches were suspended from mid-canopy branches (ca. 6 m; mid-canopy). For the suspended branches, a rope was tied to one end of each sample branch and then using the rope and various canopy branches as supports the sample branches were raised to the appropriate height and then secured. The twelve branches were left on the ground or suspended for the next 11 months, after which I collected the branches on 26 April 1987, labelled them by treatment, and took them to the USDA Forest Service laboratory on the Michigan State University campus. Each branch was placed in an individual, fine-mesh, cloth sleeve cage that was closed at each end with plastic-coated wire and maintained on a laboratory bench at room temperature. The sleeve cages were examined daily during the work week through July 1987 with all borers and parasitoids collected, placed in labelled vials, and then frozen until identified.

Results. Study 1. In 1986, which was assumed the first year after infestation of the hickory branches given that the trees died in 1985, 199 individual borers representing eight species were reared, including one bostrichid, three buprestids, two cerambycids, and two curculionids (Table 1). The three most common borers from hickory were the bostrichid *Xylobiops basilaris* (Say), the buprestid *Agrilus otiosus* Say, and the curculionid *Magdalis olyra* (Herbst) (Table 1). Considering all borers from hickory, individuals were collected from 7 May to 3 August 1986 (Table 1). Similarly, 18 indi-

Table 1. Collection data for adult bark- and wood-infesting Coleoptera (borers) and parasitoids (Hymenoptera) reared from shagbark hickory (*Carya ovata*) branches outdoors in 1986 and 1987 in Ingham County, Michigan.

FAMILY	Number collected		Collection dates (range)[1]		
Species	1986	1987	Calendar days	Julian days (mean)	Identifier[2]
Borers					
BOSTRICHIDAE					
Xylobiops basilaris (Say)	91	1	7 V–3 VIII	148-215 (156)	RAH
BUPRESTIDAE					
Agrilus otiosus Say	42	1	28 V–19 VI	148-169 (154)	SGW
Anthaxia viridifrons Gory	10		25 V–8 VI	145-159 (150)	SGW
Chrysobothris adelpha Harold	6		11 VII–12 VII	192-193 (193)	SGW
CERAMBYCIDAE					
Dorcaschema nigrum (Say)		1	13 V	133	DCLG
Molorchus bimaculatus bimaculatus Say		5	9–10 V	129-130 (130)	DCLG
Neoclytus acuminatus (Fabricius)	1		19 VI	169	DCLG
Phymatodes testaceus (L.)	2		31 V– 7 VI	151-158 (155)	DCLG
CURCULIONIDAE					
Magdalis olyra (Herbst)	38		7 V–25 V	127-145 (130)	SJK
Scolytus quadrispinosus Say	9		13 VI–19 VI	164-169 (166)	RAH
Parasitoids					
BRACONIDAE					
Doryctes sp.	3		18 V–8 VI	138 – 159 (151)	PMM
Eubazus sp.	10		13 V–17 V	130 – 137 (134)	PMM
Spathius sp.	2		27 V–31 V	147 – 151 (149)	PMM
EURYTOMIDAE					
Eurytoma phloeotribi Ashmead	2		13 V	133	RWC
ICHNEUMONIDAE					
Xorides humeralis (Say)	1		23 V	143	RWC

[1] The collection data presented are combined for both 1986 and 1987.
[2] Identifiers: DCLG = David C. L. Gosling, PMM = Paul M. Marsh, RAH = Robert A. Haack, RWC = Robert W. Carlson, SGW = Stanley G. Wellso, SJK = Steven J. Krauth.

vidual parasitoids, representing five species, were reared from hickory in 1986, including three braconids, one eurytomid, and one ichneumonid (Table 1). The most common parasitoid was an unidentified braconid species in the genus *Eubazus* (Table 1). In addition, several *M. olyra* adults had phoretic mites on their coxae that were identified by John C. Moser as *Pseudotarsonemoides* sp. (Trombidiformes: Tarsonemidae).

In 1987, the apparent second year after infestation, only eight individual borers, representing four species in three families, were collected from the hickory branches (Table 1). Neither of the two cerambycids that emerged in 1987 [*Dorcaschema nigrum* (Say) and *Molorchus bimaculatus bimaculatus* Say] had been collected in 1986. However, each of the other two species collected in 1987 (one *A. otiosus* and one *X. basilaris*) had been collected in 1986 on several occasions (Table 1).

Considering the rearing data from elm, 615 individual borers representing seven species were collected in 1986, including one buprestid, three cerambycids, and three curculionids (Table 2). The two most common borers from elm were the curculionids *Magdalis barbita* (Say) and *S. multistriatus* (Table 2). Considering all borers from elm, individuals emerged from 7 May to 2 July 1986 (Table 2). As for the parasitoids from elm, 611 individuals representing eight species were reared in 1986, including three braconids, one chalcidid, two eurytomids, one ichneumonid, and one pteromalid (Table 2). The two most common parasitoids were unidentified species of *Eubazus* and *Spathius* (Table 2). In addition, several adult weevils of *Magdalis armicollis* (Say) had phoretic mites on their coxae that were identified by John C. Moser as *Pyemotes scolyti* (Oudemans) (Trombidiformes: Pyemotidae).

Study 2. Overall, 46 borers and 36 parasitoids were reared from the 12 hickory branches that had been placed beneath or suspended in a hickory tree for nearly a year (Table 3). No borers or parasitoids

Table 2. Collection data for adult bark- and wood-infesting Coleoptera (borers) and parasitoids (Hymenoptera) reared from slippery elm (*Ulmus rubra*) branches outdoors in 1986 in Ingham County, Michigan.

FAMILY Species	Number collected	Collection dates (range)[1] Calendar days	Julian days (mean)	Identifier[1]
Borers				
BUPRESTIDAE				
Anthaxia viridifrons Gory	15	27 V–15 VI	147–166 (152)	SGW
CERAMBYCIDAE				
Neoclytus acuminatus (Fabricius)	3	8 VI–24 VI	159–175 (165)	DCLG
Saperda tridentata Olivier	11	10 V–18 V	130–138 (135)	DCLG
Urgleptes querci (Fitch)	2	4 VI–2 VII	155–183 (169)	DCLG
CURCULIONIDAE				
Magdalis armicollis (Say)	25	11 V–11 VI	142–162 (146)	SJK
Magdalis barbita (Say)	477	7 V–31 V	127–151 (137)	SJK
Scolytus multistriatus (Marsham)	82	27 V–2 VII	147–183 (170)	RAH
Parasitoids				
BRACONIDAE				
Doryctes sp.	1	29 V	149	PMM
Eubazus sp.	259	9 V–12 VI	129–163 (145)	PMM
Spathius sp.	312	8 V–1 VII	128–182 (160)	PMM
CHALCIDIDAE				
Trigonura ulmi Burks	1	1 VI	152	RWC
EURYTOMIDAE				
Eurytoma conica Provancher	9	1 VI– 19 VI	152–170 (157)	RWC
Eurytoma phloeotribi Ashmead	13	25 V–15 VI	145–166 (159)	RWC
ICHNEUMONIDAE				
Xorides albopictus (Cresson)	11	9 V–22 V	129–142 (134)	RWC
PTEROMALIDAE				
Cheiropachus quadrum (Fabricius)	5	30 V–31 V	150–151 (151)	EEG

[1] Identifiers: as given in footnote 2 in Table 1 with the addition of EEG = Eric E. Grissell.

were reared from the branches placed on the ground, compared with 17 borers and 7 parasitoids collected from branches in the lower-canopy, and 29 borers and 29 parasitoids from branches in the mid-canopy (Table 3).

Discussion. As trees die and decay, there is a succession of borers, parasitoids and other associated insects that colonize the woody tissues (Haack and Slansky 1987, Hanula 1996, Grove 2002). Several studies have documented insect succession in decaying logs and branches of specific tree species, including species of *Carya* (Blackman and Stage 1924), *Larix* (Blackman and Stage 1918), *Pinus* (Savely 1939), *Quercus* (Savely 1939), *Tilia* (Townsend 1886), and *Ulmus* (Tucker 1907, Marković and Stojanović 2012).

Species of *Carya* and *Ulmus* are known larval hosts for all the borers reared in the present study (Packard 1890, Felt and Joutel 1904, Felt 1905, Blackman and Stage 1924, Gosling 1973, 1984, Wellso et al. 1976, Solomon 1995). In fact, all borers reared in this study from *C. ovata* have been previously reported from *C. ovata*. Similarly, all borers reared in this study from *U. rubra*, except one, have been previously reported from *U. rubra*. The one exception is the cerambycid *Urgleptes querci* (Fitch), which has been reared from many hardwood tree species, including American elm (*Ulmus americana* L.) (Gosling 1984, MacRae 1993), but I did not find any published records of this beetle being reared from *U. rubra*. The emergence data for the borers reared in this study agree broadly with the seasonal adult activity periods reported by others for these same species (Felt 1905, Yanega 1996, Solomon 1995).

As for new state records for Michigan, I have found in-print published Michigan records for all the borers presented in this study (Gosling 1973, Gosling and Gosling 1977, Wellso et al. 1976, Downie and Arnett 1996, Cognato et al. 2009, and many additional online searches using Google Scholar through November 2020), except the bostrichid *X. basilaris*. However, using the online SCAN database (https://scan-bugs.org/) in November 2020, which contains collection records of insects from over 100 North American arthropod collections,

Table 3. Number and dimensions of shagbark hickory (*Carya ovata*) branches that were cut in May 1986 from a healthy tree and placed at one of three positions at the base of or in the canopy of another hickory tree until April 1987 when taken indoors for rearing any associated borers and parasitoids that were present (see Methods for details).

	Branch location		
Parameter	**Ground level**	**Lower canopy**	**Mid-canopy**
Branch data			
Number	4	4	4
Diam at cut end, range (cm)	2.1–4.4	3.1–5.4	1.9–5.3
Length, range (m)	1.2–1.7	1.6–1.8	1.3–2.0
Number of borers reared[1]			
Xylobiops basilaris (Say)	0	12	18
Agrilus otiosus Say	0	5	11
Number of parasitoids reared[1]			
Doryctes sp.	0	2	1
Eubazus sp.	0	0	3
Spathius sp.	0	5	24
Eurytoma phloeotribi Ashmead	0	0	1

[1] The numbers of borers and parasitoids are the total number of individuals reared for all four branches that were at each location.

Michigan specimens of *X. basilaris* have been deposited at the A. J. Cook Arthropod Research Collection (ARC) at Michigan State University (MSU), as well as on BugGuide.net (photo # 604222). With respect to the six parasitoids that were identified to the species level, I found in-print published Michigan records for only two species, including the chalcidid *Trigonura ulmi* Burks (Rowher 1920, Shaddy et al. 1978) and the ichneumonid *Xorides albopictus* (Cresson) (Krombein et al. 1979). For the other four parasitoids, I found no in-print published records, nor any Michigan records in the SCAN database or on BugGuide.net and therefore the following parasitoids are considered new state records for Michigan; the eurytomids *Eurytoma conica* Provancher and *Eurytoma phloeotribi* Ashmead, the ichneumonid *Xorides humeralis* (Say), and the pteromalid *Cheiropachus quadrum* (Fabricius).

The borers and parasitoids listed in Tables 1 and 3 all emerged the year after the host material was apparently first infested, indicating a univoltine life cycle for these species. The two *A. otiosus* and *X. basilaris* adults that were reared from hickory branches two years after their apparent initial infestation suggests that these two species can have a 2-year life cycle at times. A 2-year life cycle for borers that are typically univoltine can occur when eggs are laid in late summer, and thus the resulting larvae require two seasons of feeding before being able to pupate. Also, if the host material becomes excessively dry, larval development time can be protracted, which can delay adult emergence by a year or more (Haack and Slansky 1987, Haack 2017). For example, the buprestid *Agrilus planipennis* Fairmaire is typically univoltine, but a 2-year life cycle was recorded for some individuals reared from cut firewood (Petrice and Haack 2007). By contrast, the two cerambycid species (one *D. nigrum* and five *M. b. bimaculatus*) that emerged from hickory branches in 1987, but for which none emerged in 1986, may commonly have a 2-year life cycle. In support of this contention consider the rearing data of Blackman and Stage (1924), who collected insects from trunk and branch sections of hickory trees in New York that had died 1-6 years earlier, which also indicated a 2-year life cycle for both *D. nigrum* and *M. b. bimaculatus*.

I did not attempt to associate the parasitoids reared in this study with their insect hosts. However, based on other studies, largely summarized in Krombein et al. (1979), the braconids, chalcidids, eurytomids, and pteromalids reared in this study are common parasitoids of many bark beetles (Curculionidae: Scolytinae) and weevils in the genus *Magdalis*. Similarly, ichneumonids in the genus *Xorides* are common parasitoids of cerambycid larvae. In fact, *X. albopictus* has been reared from *S. tridentata*, and *X. humeralis* has been reared from *Phymatodes testaceus* (L) and *Neoclytus acuminatus* (Fabricius) (Krombein et al. 1979) – all three (cerambycids) of which were reared in the present study (Tables 1-2). Some of the parasitoids reared in this study could also have used the bostrichids and buprestids as hosts, given that they were the most common borers reared from hickory

(Tables 1 and 3), and that several families of hymenopteran parasitoids have been reared from various *Agrilus* and *Xylobiops* species (Krombein et al. 1979, Petrice et al. 2009, Taylor et al. 2012, Bertone et al. 2017).

Vertical stratification has been reported for many forest insects, with some favoring the canopy of trees to search for food, hosts and oviposition sites, while others search mostly in the understory (Ulyshen 2011). Variation in vertical distribution has been documented for both borers and parasitoids (Pucci 2008, Hardersen et al. 2014, Di Giovanni et al. 2015, Rassati et al. 2019, Sheehan et al. 2019). Given that the hickory branches used in the present study were more heavily infested by both borers and parasitoids when placed in the canopy than on the ground, suggests that the insects listed in Table 3 display vertical stratification when searching for suitable host material.

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SUBJECTS

Papers dealing with any aspect of entomology will be considered for publication in The Great Lakes Entomologist. Appropriate subjects are those of interest to professional and amateur entomologists in the North Central States and Canada, as well as general papers and revisions directed to a larger audience while retaining an interest to readers in our geographic area. All manuscripts are refereed by at least two reviewers.

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Footnotes (except for authors' addresses, which must be on the title page, and treated as a footnote), legends, and captions of illustrations should be on separate pages.

Titles should be concise, identifying the order and family discussed. The author of insect species must be given fully at least once in the abstract and text, but not in the title. If a common name is used for a species or group, it should be in accordance with the common names published by the Entomological Society of America, or the Entomology Society of Canada.

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Photographs should be high resolution digital files (300 dpi). Drawings, charts, graphs, and maps must be scaled to permit proper reduction without loss of detail.

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